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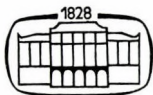
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SIXTY YEARS ACTIVITY OF PROF. BÁLINT ZÓLYOMI IN THE FIELD OF PLANT ECOLOGY*

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It is more than sixty years since a short article appeared in the journal "Youth and life". A young man of 19, not long before a secondary school student at Győr gave a precise description, a brief characterization of the sand vegetation of Győr county at that time. Sándor POLGÁR, the beloved teacher soon noticed the extraordinary talent and vocation of his pupil, and encouraged and guided him. But perhaps even he did not foresee ZÓLYOMI's rich future career.

When greeting the eighty years old Bálint ZÓLYOMI we cannot survey the full range of his professional activity, so we pick out some important phases from his work in the field of plant ecology, suitably to the topic of the congress. The examples we are going to speak had greatly influenced or even determined the pupils' views and the direction of their research work.

Bálint ZÓLYOMI's whole synbiological activity is fundamentally determined by an ecological mentality. For him field work and field experience are more important than anything else. His observations are always exact, he recognizes and properly evaluates the discontinuities, the relevant units in the vegetation. His surveys are precise, exemplary. The necessity of interpretation, of exposing the ecological background arises in every case. Early convincing syntheses of field observations are the succession-schemes representing the dynamics of bogs and marches. Relying on his own observations concerning vegetation dynamics ZÓLYOMI gave an accurate description of the effect of human activity on the march vegetation in the basin of the Hanság (a region in North-West Hungary around Lake Fertő) at the very beginning of the thirties. It is astonishing how precisely

*A written version of a lecture given at the First Congress of Ecologists Budapest, 27. 4. 1988

he prognosticated the unfavourable changes which — as we now know — took place at a speed and rate even higher than expected with the extensive drainage work of the Hanság. The basic tendencies he recognized in and the explanations he gave for the dynamism of the hydroseries of Szigetköz (Area between two branches of the river Danube in North-West Hungary) are valid even today.

ZÓLYOMI's suggestivity is a mobilizing force. He was able to convince his colleagues working in other fields about the importance of plant ecological problems. For example, after it had become obvious for him that it is the microclimate which is responsible for the formation of montane or cool continental vegetation types and the survival of rare relics he persuaded Nándor Bacsó in 1934 to carry on biometeorological measuring. Leading pedologists of those days were also glad to co-operate with him. He regarded the soil as a formation developing parallel with the vegetation. When diagnosing and mapping he made use of the lucky cases when the categories coincided. His outstanding results include the demonstration by a vast material of the close correlation between the occurrence of *Lithospermum purpureo-coeruleum* and the Ca^{++} -ion.

An area important for him up to now has been the sociology and ecology of forests. Few know the forests of South-Eastern Europe better than ZÓLYOMI. It is here that the great knowledge resulting from field experiences, sociological and chorological studies and from the knowledge of habitat is in its proper place. He also differed from his sociologist contemporaries in quickly realizing that the species composition of the European forests was greatly influenced by the practice of forest management. Therefore — then already over forty — he set to learning silviculture. It was not by mere chance that in the fifties Bálint ZÓLYOMI was that sociologist who was able to have himself and his profession accepted by the foresters. He had much to do with the fact that that period was the golden age of forest typology in Hungary, when the silvicultural practices were based on a forest sociology of ecological view. The first attempts of ordination of the forest types were made at that time. For the young professional as I was then it was an experience for life to be a member of the team who under ZÓLYOMI's guidance were the pioneers of sociological mapping in Hungary. The results of this work brought him the official appreciation: the Kossuth Prize. The novelties of sociological mapping can be placed in four groups. A large number of reliable examples were listed to show the relations of vegetation — soil type; the examples of fidelity were properly

documented; the theory of zonality was substantiated (see: exposition diagrams); the connection between phytocenology and forest management was established.

ZÓLYOMI's concept of the vegetation shows a manifold dynamism. In the case of anthropogenic changes it is a matter of small-scale dynamics. The large-scale dynamic is represented by the secular succession. On this question ZÓLYOMI has been the great authority up to the present day. His palynological studies give not only the reconstruction of postglacial event in vegetation, they are at the same time excellent palaeoecological works. His papers which show a strong historical sense offer much new for palaeogeography, archeology, agricultural history; these sciences need his palynological collaboration even today.

One of his favourites is the vegetation of the Buda-hills. The monograph published in 1958 has remained the best work on the vegetation of Hungary up to the present day. It is a unique synthesis of all that can be said with a knowledge of vegetation history, climatology and sociology. It shows what the possibility provided by a pool of climatic data for the interpretation of the phenomena of vegetation is, though — as it is also pointed out — a climatological view is not enough by itself. That only the ecologist is able to choose the relevant elements of climate is clearly shown by Bálint ZÓLYOMI's example. ZÓLYOMI introduced his method of climatic statistics examining the frequency distribution of the different climatic year-types. This way of looking at the phenomena of vegetation brought him the first success in 1942 (see: Mid-Danubian flora parting and the dolomite phenomenon) when he gave explanation for the distribution of submediterranean and continental species in Hungary.

ZÓLYOMI anticipated the changes of times and when necessary was capable of switch-over. It so happened in the mid-sixties when the International Biological Programme found its way into Hungary. The results of his researching, guiding and managing activity are the novelties linked with the names of the research workers at the Botanical Research Institute of the Hungarian Academy of Sciences. At that time already a new generation of researchers worked, new production-ecological sampling and evaluating methods were introduced and developed. It became clear then how important the steps taken by Prof. Imre MÁTHÉ and his colleagues for the early introduction of production ecology in Hungary were. During the International Biological Programme an exemplary co-operation was brought about between them.

A study in which he elaborated the principle and practice of the so-called TWR-indicator numbers has been for about ten years perhaps his most often cited work abroad. The greatest merit of the paper is the consequent application of a conception by which he has succeeded in ranking — with a collective work — almost the whole Hungarian flora over three scales. In fact, in this undertaking experiences of a long life are concentrated. While ZÓLYOMI used many sociological tables, another important — and equally reliable — source of categorization and weighing were the tens of thousands of cases and field observations which — somehow worked up — remained indelibly graven on his memory.

The above account, however short and sketchy, gives some idea of the lines on which Bálint ZÓLYOMI has broadened and shaped our views, though hardly any mention has been made of his phytosociological activity. He is a real expert of the Hungarian vegetation — as shown by the reconstructed vegetation map of Hungary, ZÓLYOMI's work adopted for text-books, manuals, etc. as an indispensable fundamental work. But perhaps his favourite, ever returning subject is the cenogenetics of dolomite rock swards and karstic beechwoods rich in relics.

The picture would not be complete if only the scientist were presented. ZÓLYOMI always has done his best to make good use of his knowledge for the benefit of the society. The establishment of forest typology has been mentioned already. And it was his love for the forests that moved him to stand up passionately against the abuses of forest management in the recent years. According to his widely propagated opinion our future and the welfare and interests of our descendants are endangered by the extreme industrial mentality concerning the use of forests. ZÓLYOMI hates the merciless technocratic attitude towards nature. He spares neither energy nor time to set forth his views in newspapers and journals too. He is well informed in important or critical questions of nature conservancy and environment protection and even knows the momentary position of protracted debates. His well-considered opinion can always be relied upon.

ZÓLYOMI's whole activity reflects a passionate commitment. It is a legacy he has proudly accepted from his teachers, first of all from Sándor JÁVORKA and from his great contemporaries, to give it over to the following generations. He is lucky to have begun his career in an early stage of the science of geobotany, when he could freely evolve his personality and vocation without the restrictions concomitant with the present high degree of specialization.

Searching for truth and an unconditioned love for science are the chief traits that have characterized him in all his life, and from which he has taken courage in the most critical situations giving us an example for life.

We wish Prof. Bálint ZÓLYOMI many more happy creative years and good health!

Papers of Prof. dr. B. Zólyomi since 1979

For the first part of the list of his publications see: *Acta Bot. Hung.* 26: 7–14. 1980.

Zárszó (Closing lecture) – *MTA Biol. Oszt. Közlem.* 22, 1979, p. 441–442.

Soó Rezső 1903–1980. – *Magyar Tudomány* (87) 25, 1980, p. 697–699. 1 kép
Wissenschaftliche Publikationen und andere Mitteilungen von dr. Bálint Zólyomi – Acta Biologica Academiae Scientiarum Hungaricae 26, 1980, p. 7–14.

Hozzászólás Láng I.: Beszámoló az agroökológiai potenciál országos felméréseinek eredményeiről c. előadásához (1980. V. 6.) (Contribution to the lecture by Láng. I.: Account of the results of a nation-wide survey of the agroecological potential) – *MTA Agrártudományi Közlem.* 40, 1981, p. 56–57.

Természetes erdők, mesterséges állományok (Vitarovat) (Natural forests, artificial stands) – *Bot. Közlem.* 68, 1981, p. 133–136.

Ézsau tál lencséje és az ökológia (Esau's mess of pottage and the ecology) – *Magyar Nemzet* (1981. IX. 18.) p. 9.

Magyarország természetes növénytakarója 1:1 500 000 térkép. Kartográfiai Vállalat (1981). Melléklet: a) Növényföldrajz, társulástan és ökológia egyetemi tankönyvhöz (1981). Önálló is. (Natural vegetation of Hungary 1:1 500 000 map – Cartography Enterprise) (1981). Appendix: a) Plant geography (phytogeography), sociology and ecology for a university text-book (1981). Complete by itself.

Professor Imre Máthé 80 years old
– *Acta Botanica Academiae Scientiarum Hungaricae* 27, 1981, p. 281–284. 1 kép

Bulla Béla, a pályatárs (Béla Bulla, the colleague) – *Földrajzi Közlemények* (106), 30, 1982, p. 371–372.

Vallomások Szegedről (Confessions) statements? (on Szeged) – *Somogyi-könyvtári műhely* (Somogy county library) – 22, 1983, p. 197–198.

Hozzászólás: (Kedves Élet és Tudomány). (Contribution) – *Élet és Tudomány* 38, 1983, p. 1154, 1175.

Jávorka Sándor és a természetvédelem (Sándor Jávorka and the nature conservancy) – *Búvár* 38, 1983, p. 221. 1 kép

Sándor Jávorka born 100 years ago – *Acta Botanica Hungarica* 29, 1983, p. 5–12. 1 kép

- Alpesi fény Budapesten (Béll Bélával közösen). (Alpenglow in Budapest) (Afterglow in Budapest?) – Természet Világa 115, 1984, p. 18–21. 4 ábra
- Hetvennyolc év virágporban elbeszélve (Barabás Zoltán kérdéseire válasz). (Seventy-eight years as told in pollen) – Élet és Tudomány 39, 1984, p. 486–487. 1 kép
- A flóra- és vegetációkutatás története a Bükk-hegységben. (History of flora- and vegetation research in the Bükk mountains) (North-Eastern Hungary) – Az Erdő 119, 1984, p. 245–249.
- A megmentett sziklasüveg. (The rock-cap rescued) – Képes Újság 26, 1985. II. 23. 8, p. 2–3. 1 kép
- Pollenstatistische Analyse der Teichablagerungen des Mittelalterlichen Klosters bei Pilisszentkereszt. Vergleich mit dem Grundprofil des Balaton (mit I. Précsényi) – Acta Archaeologica Academiae Scientiarum Hungaricae 37, 1985/1986, p. 153–158. 1 diagr.
- A Bükki Nemzeti Park szigorúan (fokozottan) védett területeinek botanikai és zoológiai jellemzése. Javaslatok VÁTI BNP regionális és tájrendezési tervéhez (Jakucs P.-lal és Varga Z.-nal közösen). A Bükki Nemzeti Park regionális és tájrendezési terve. Konceptió. (1985) 1. sz. melléklete 1–77. Sokszorosítva 140 példány. (Botanical and zoological characterization of the strictly protected areas of the Bükk National Park. Suggestions for the VÁTI BNP regional- and country planning) (in co-operation with Jakucs P. and Varga Z.) Regional- and landscape plan for the Bükk National Park. Conception (1985). Appendix No. 1. pp. 1–77. 140 copies.
- Foreword. In: Ecology of an oak forest in Hungary (ed.: P. Jakucs). – Akadémiai Kiadó Bp. 1985. (1986) p. IX. 1.
- Vallomások tudósokról – "Érdekes az is, amit más csinál" Zólyomi Bálint – Jávorka Sándorról és Soó Rezsőről. (Confessions on scientists – "Somebody else's doings are also interesting" Bálint Zólyomi on Sándor Jávorka and Rezső Soó) – Magyar Tudomány, 1986, 10, p. 807–812.
- Körgyűrűben (autópálya) a tájvédelmi körzet? (Landscape protection district in ring?) – Élet és Tudomány, 1987 (42), III. 27. 13. sz. p. 407.
- Proceedings of the IAB Conference of Bryoecology (1985) 1987, Begrüßungsansprache, Könyvrészlet XV–XVI.
- Buntflechten – Moos und Lebermoos Synusien – Könyvrészlet. Symposia Biologica Hungarica 35, 1987, p. 375–378.
- Degree and rate of sedimentation in lake Balaton – (Kanadai kongresszus) 1987. Fig. 6, p. 57–79. – In Pécsi, M. (ed.) Pleistocene environment in Hungary, könyvrészlet
- Coenotone, ecotone and their role in the preservation of relic species. 1987. – Acta Botanica Hungarica 33, pp. 3–18, Fig. 7.
- Az ökológiai indikátorszámok mintázatának változása szukcesszió alatt. (Changes in the patterns of ecological indicator values in the course of succession) – Botanikai Közlemények 1987. – Zólyomi B. – Précsényi, I. – Bodnár, T. – Vadkerti, E.
- Emlékezés dr. Polgár Sándorra, a tudós tanárra – Révai Miklós Gimn. 200 éves jubileumi értesítő. (Reminiscences of Sándor Polgár dr., the

teacher of profound learning. — Second centenary school report of the Révai Miklós Gymnasium.) — 1988, p. 5, figs 3

A som elterjedése és társulásviszonyai (Jakucs P.-lal közösen) (Distribution and sociology of corn) (With Jakucs P. as co-author) — Magyarország Kultúrflórája, könyvrészlet

Indirecte Methode zur Feststellung des ökologischen Optimum (u. Toleranzbreite) von Pflanzenarten. 1988. Flora (Jena), figs 3

LOKALE INDUSTRIELLE EMISSION UND WALDSCHÄDEN IN NORDUNGARN I.
PROBLEMSTELLUNG, AUSGANGSHYPOTHESE UND ZUSAMMENFASSENDE WERTUNG

JAKUCS, P. — BERKI, I. — HOLES, L. — TÓTHMÉRÉSZ, B.

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Healthy and diseased sessile oak individuals and the soil were studied in the surroundings of heavily polluting industrial establishments of North-East Hungary and in increasing distance from this area. To the chemical parameters of the soil and leaves the paper of BERKI and HOLES, to the symbiotic relations between the mycorrhiza and the thin roots the paper of HOLES and BERKI, while to the width of annual rings in the trunks and to the obstruction of the tracheae the paper of JAKUCS and BABOS (all in this volume) contribute more detailed information. In this paper the study area the quantity of the emitted SO_2 , NO_x , NH_4 , chlorine and solid pollutants are described. Twenty-seven different parameters were statistically evaluated. The goal of the study was to find correlation between the values indicating the degradation of the forest stands, characteristic of the ecophysiological state of trees and the increasing distance from the emitting sources by means of an integrated analysis. They found that the local industrial air pollution influences drastically the processes of the tree die-back and results in the decrease of the stability of forests near the factories. The local industrial air pollution increases the effect of the long-distance polluting materials acting through the soil and remarkably accelerates the degradation processes of forests (including the tree decline as well).

EINFÜHRUNG

Die Wirkung der trockenen oder nassen Sedimentation von Luftschadstoffen anthropogener Herkunft auf Pflanzen und Boden wird auf der ganzen Welt intensiv untersucht (ULRICH et al. 1979, HUTCHINSON und HAVAS 1980, SMITH 1981, PRINZ et al. 1982, ULRICH und PANKRATH 1983, SCHÜTT 1984, SCHÜTT und COWLING 1985, McLAUGHIN 1985, KARL-URBAN et al. 1987, KLEIN und PERKINS 1987, WOODMAN und COWLING 1987, etc.).

In den vergangenen 10 Jahren wurden in Ungarn die Wälder der Traubeneiche (Quercus petraea s.l.) am meisten geschädigt. 1985 standen in den Eichenwäldern von Ungarn bereits bis zu 20.5% ausgetrocknete Bäume: im

Mittelgebirge von Nordungarn bis 26,4%, in Transdanubien 9.9% und in der an die Alpen angrenzenden schmalen Zone bis 5.6% (IGMÁNDY et al. 1986). Diese Werte erhöhten sich seitdem kontinuierlich, der Absterbevorgang erreichte in einigen Waldabschnitten den Wert von 80–100%. An anderen Stellen ist der Vorgang wiederum stagnierend oder er zeigt eine mässig ansteigende Tendenz.

Aufgrund der früheren ökologischen Forschungen lässt sich feststellen, dass bei Laubbäumen als primäre Schädigungsursache die Luftverschmutzung betrachtet werden kann. Durch die Luftschadstoffe wird nämlich die Versauerung des Bodens und dadurch die Veränderung des Mineralstoffgleichgewichtes im Boden hervorgerufen (JAKUCS ed. 1983, MÉSZÁROS 1984, JAKUCS et al. 1986, JAKUCS 1988).

Die Werte der Luftschadstoffemission des sog. Industriegebietes Sajó-Tal in Nordungarn sind um das vielfache höher, als die des Landesdurchschnittes sowie die der Hintergrundverschmutzung. Diese Werte können sich ausserdem auch addieren. Das "neuartige" Absterben der Quercus petraea-Bäume in diesen Wäldern begann in den Jahren 1977/78. Heute sind über 50% der Bäume bereits abgestorben und ein Teil der noch stehenden ist "erkrankt". Diese Gegend ist eine der am stärksten geschädigten Waldgebiete Ungarns.

Zum Nachweis der waldschädigenden Wirkung der starken, lokalen Emission wurden in der Nähe der Emissionsquellen und davon entfernter komplexe ökologische Untersuchungen durchgeführt, in welchen ständig die gleichen "gesunden" und "kranken" Bäume sowie ihr Mikromilieu analysiert worden sind.

Folgende Parameter wurden untersucht:

- Mineralstoffgehalt der Böden und der Blätter der Bäume (BERKI-HOLES 1988),
- Gestaltung der symbiotischen Mykorrhiza-Beziehungen des Wurzelwerkes (HOLES and BERKI 1988),
- Jahrringbreiten sowie Thyllenverstopfung von wasserleitenden Gefässen der Stämme bei gesunden und erkrankten Bäumen (JAKUCS and BABOS 1988),
- Umfang des Baumsterbens in den ausgewählten Waldabschnitten, indikative Unkrautbeschaffenheit der Bodenvegetation.

Die vorliegende Studie stellt eine Synthese unserer zusammengefassten Ergebnisse dar.

UNTERSUCHUNGSGEBIET

An das Bükk-Gebirge in Nordungarn schliesst sich eine auf 300 bis 400 m ansteigende Hügellandschaft entlang des Flusses Sajó an, welche aus Ablagerungen des Miozäns aufgebaut und mit dem Lehm des Pleistozäns bedeckt wurde. Die Quercus petraea – Qu. cerris Phytozönosen bilden die natürlichen klimazonalen Wälder dieser Hügellandschaft.

Die etwa 15x25 km grosse Hügellandschaft wird im Norden und Osten vom breiten Alluvium des Flusses Sajó begrenzt. Hier entwickelte sich seit 1950 das sog. "Industriegebiet im Sajó-Tal", in welchem fünf grossen Industriekomplexe zu den potentiellen, starken Luftverschmutzern gehören (Kazincbarcika und Sajóbáony: Kunstdünger- und Chemieindustrie; Berente: Heizkraftwerk; Sajókerezstúr: Erzvorbereitung; Miskolc-Diósgyőr: Eisenhüttenindustrie). Nach eigenen Angaben der fünf genannten Grossbetriebe war der Emissionsausstoss bezüglich 4 verschiedener Luftschadstoffe in den Jahren 1978–1986 folgender: Schwefeldioxyd 65 389 t/Jahr; Kohlenmonoxyd 67 730 t/Jahr; nitrose Gase 6 753 t/Jahr; Ammoniak 2 219 t/Jahr. Ein bedeutender Teil dieser Schadstoffe wird aufgrund der Witterungsverhältnisse (Windrichtung- und -stärke, Nebel usw.) jährlich mehr als 6 Monate über das Untersuchungsgebiet getrieben, wo er dann in Form von trockener oder nasser Sedimentation letzten Endes in den Boden der Wälder gelangt.

Die Probeentnahme erfolgte in 9 Waldbeständen in einem 0.5 bis 12 km breiten Umkreis der emittierenden Quellen. Innerhalb der einzelnen Waldbeständen wurden von den einander nahe stehenden "gesunden" und "kranken" Bäumen (Verminderung der Blattmasse, Gelbfärbung der Blätter, vertrocknete Aste usw.) Proben entnommen. Die Probeentnahme erfolgte vom 15. bis 19. Juli 1987.

Die einzelnen Probeentnahmestellen werden in der Abbildung 1. dargestellt, die wichtigsten Daten der untersuchten Beständen zeigt die Tabelle 1.

Während die Laubkrone im Wesentlichen überall noch die Artenzusammensetzung der ursprünglichen Quercetum petraeae-cerris Phytozönose zeigte, wurden in der Strauchschicht und vor allem in der Krautschicht beherrschende Unkräuterarten (hauptsächlich Nitrophyte) beobachtet, was auf die starke Degradierung dieser Wälder hinweist.

Als Kontrolle wurden von uns die Bäume von zwei gesunden Quercetum petraeae-cerris Beständen geprüft, die etwa 18 bis 35 km entfernt von den

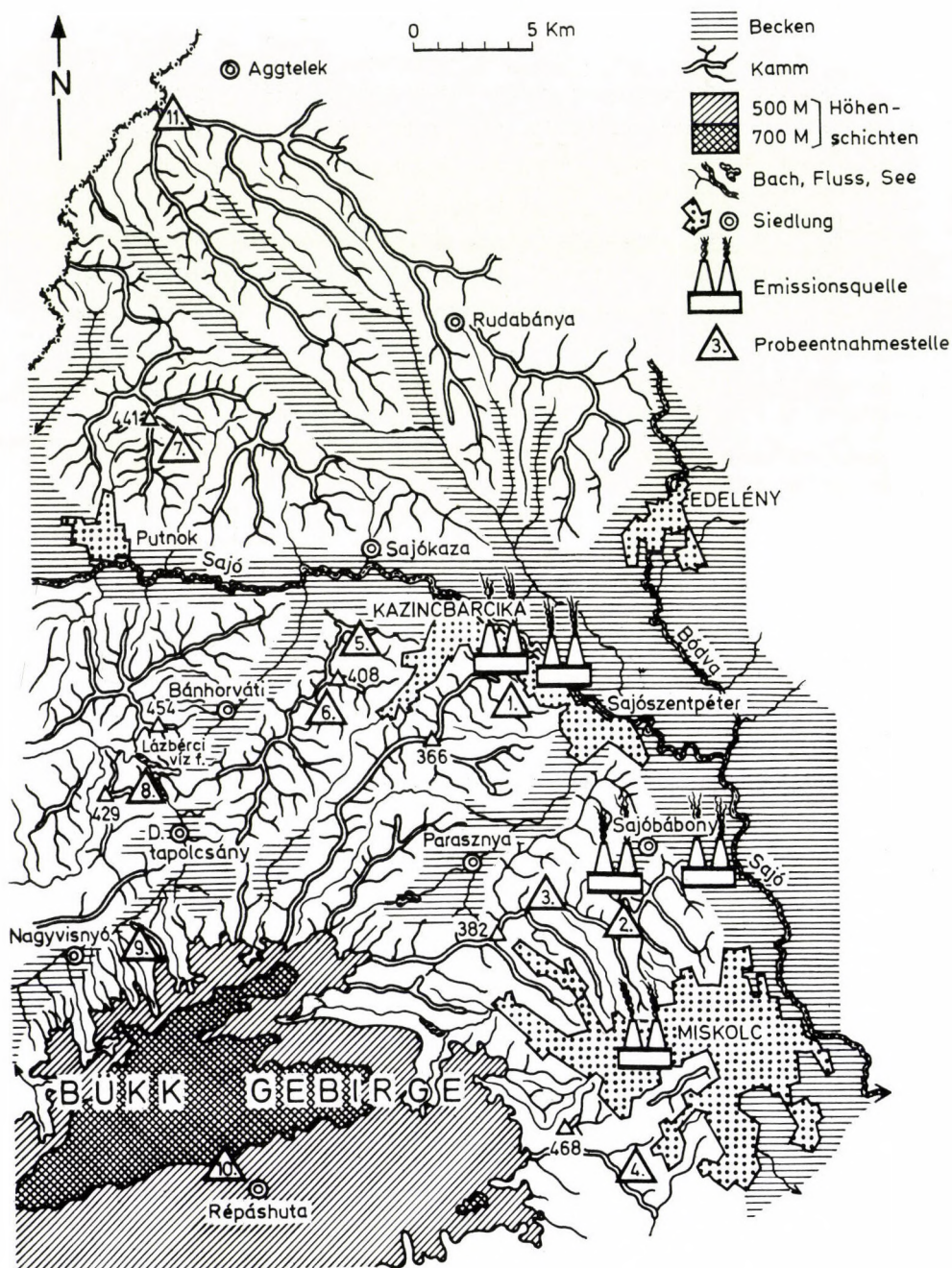


Abb. 1. Untersuchungsgebiet mit den Probeentnahmestellen und luftverschmutzenden Industriegebieten

Tabelle 1

Die wichtigsten Daten der Bestände auf den Probeentnahmestellen

Kod- zahl	Name der Siedlung, Kodzahl des Waldabschnittes, Höhe über d. Meer	Entfer- nung d. nächsten Emissions- quelle	Qu.p.- Abster- ben im	Expo- siti- on	Neigungs- winkel	Begleiten- de Bäume	dominierende Unkräuter		Ver- hältnis Unkraut/ ursprüng- liche Arten
	(m)	(km)	(%)				Sträucher	Kräuter	
Industriegebiet im Sajó-Tal									
1	Berente, 47/A, 250	0.6	65	N	10	Qc,R,T	R,Sam	U,Ch,Eu,G	90/10
2	Sajóbábony, 3/A, 240	0.7	60	N	10	Qc	Rub,Ros, Same	U,Ph,Con,Ger, Eu,G	90/10
3	Radostyán, 5/C, 250	2.5	45	N	5	C	Sam,Rub	U,Eu,Ch,Gal	75/25
4	Tapolca, 128/M, 360	2.6	30	-	-			U,Rub,A,Gal	50/50
5	Sajóivánka, 10/C, 350	3	60	-	-	Qc,R	Sam,Rub,R	U,S,Con	85/15
6	Kazincbarcika-Ibolyás, 11/G, 380	4	40	N	10		Rub	G,U,C	85/15
7	Putnok, 23/C, 300	10	55	-	-		Rub	Cal,U,Con	80/20
8	Dédestapolcsány-Lázberc, 360	12	60	NO	10	Qc	Rub,Ros	U,A,Ch,Gal, Con	80/20
Kontrollgebiete									
9	Nagyvisnyó-Várerdő, 360	18	3	SW	15				5/95
10	Répáshuta, 540	30	0	-	-				0/100
11	Trizs, 58/A, 350	35	0	-	-				0/100

Abkürzungen: Bäume: Qu.p. = Quercus petraea, Qc = Qu.cerris, R = Robinia pseudoacacia, T = Tilia platyphyllos, C = Carpinus betulus. Sträucher: Sam = Sambucus nigra, Same = S. ebulus, Rub = Rubus caesius, Ros = Rosa canina.
 Kräuter: U = Urtica dioica, Ch = Chelidonium majus, Eu = Eupatorium cannabinum, G = Galeopsis speciosa, Con = Convolvulus arvensis, Ger = Geranium robertianum, S = Solanum nigrum, Gal = Galium aparine, A = Alliaria petiolata,
 C = Circaea lutetiana, Ph = Phytolacca americana, Cal = Calamagrostis epigeios

Luftverschmutzungsquellen liegen. Dieses Gebiet verfügt über ähnliche geomorphologische Gegebenheiten und Bodenverhältnisse.

DISKUSSION

Aufgrund der bereits ausführlich bewerteten Daten, welche mit den bei BERKI und HOLES (1988), HOLES und BERKI (1988) und JAKUCS und BABOS (1988) beschriebenen Methoden erhalten worden sind, stellten wir eine Grundtabelle auf (Tabelle 2). In dieser Tabelle wurden in Reihenfolge (1-11) der zunehmenden Entfernung von den Emissionsquellen ausgewählten Daten gezeigt, welche in der physiologischen Abschwächung der Bäume eine prädisponierende Rolle spielen könne, bzw. welche selber die Art der Degradation indizieren. Die Werte stellen meistens den Mittelwert mehrerer Messungen dar. In den industrienahen Gebieten wurde mit den Durchschnittswerten von gesunden und kranken Bäumen gearbeitet.

Bei den Bodenanalysen wurden neben den Parametern der Bodenversauerung (pH-Wert mit zwei verschiedenen Methoden ermittelt, hydrolytischer und austauschbarer Säuregrad, Ca/Al-Verhältnis) die Werte von NO_3^- -N, Al und Ca hervorgehoben, jeweils auf eine Bodentiefe von 10 bis 30 cm bezogen. Darüber hinaus wurden auch die gemessenen Al- und Pb-Werte in dem obersten 0 bis 10 cm tiefen Bodenhorizont aufgezeichnet. Durch diese 10 Parameter individuell oder gemeinsam betrachtet wird die Gleichgewichtsstörung im Boden der industrienahen Gebiete noch anschaulicher angezeigt.

In der Tabelle 2 sind im weiteren 11 Parameter der chemischen Blattanalysen aufgeführt, unter ihnen die wichtigsten Nähr- und Makroelemente, sowie die Werte der Ca/Al- und N/P-Verhältnisse.

Beim Verhalten der Bäume und der Wälder sind die Werte bezüglich der Mykorrhiza-Beziehungen sowie die Raten der Tracheenverstopfung Indikatoren für eine Abschwächung der Toleranz der Bäume. Der prozentuale Wert der Unkrautbeschaffenheit zeigt, in wieweit die Arten der ursprünglichen Phytozönose durch nitrophyte Kräuter abgelöst wurden. In den untersuchten Beständen wurde die Menge an abgestorbenen Bäumen ebenfalls in Prozent angegeben.

Diese insgesamt 27 Parameter wurden mittels verschiedener statistischer Methoden miteinander verglichen um festzustellen, in wieweit der "ökologische Zustand" der unterschiedlich geschädigten bzw. gesunden (Kontroll) Bäume voneinander abweicht. Sicherlich spielen alle ermittelten

Tabelle 2

Gemessene Werte einiger, den ökophysiologischen Zustand der Bäume beeinflussenden und die Degradierung des Waldes anzeigende Parameter im Bezirk des Industriegebietes im Sajó-Tal (1-8) und an ferner liegenden untersuchten Stellen (9-11)

	1	2	3	4	5	6	7	8	9	10	11
Bodenchemische Parameter (Tiefe 10-30 cm)											
pH(H ₂ O)	3.550	3.630	3.690	3.840	4.110	3.880	3.980	4.240	3.970	4.230	4.890
pH(KCl)	3.450	3.300	3.120	3.110	3.280	3.180	3.090	3.260	3.390	3.490	3.600
Y ₁	49.450	27.430	51.190	54.720	41.050	45.860	24.730	68.550	31.540	38.130	14.820
Y ₂	37.100	17.360	39.590	44.120	27.560	21.140	12.180	22.270	12.530	19.440	12.270
Al (0-10) ppm	1091.500	718.400	943.400	853.000	1188.000	1081.000	572.800	620.400	683.200	635.400	259.200
Al ppm	1101.300	482.000	1075.000	1216.500	798.200	885.200	518.200	720.500	671.600	922.200	263.200
Ca/Al	0.162	0.218	0.188	0.233	0.834	0.556	0.179	1.558	0.266	0.159	2.077
NO ₃ ⁻ ppm	18.150	18.700	1.500	1.450	10.000	28.200	3.650	11.550	1.200	1.300	1.100
Pb ₃ (0-10) ppm	24.550	37.100	28.440	47.830	41.760	22.290	36.210	31.270	18.380	24.260	14.620
Cd ppm	0.070	0.046	0.024	0.108	0.064	0.048	0.032	0.072	0.030	0.024	0.029
Blattchemische Parameter											
K %	0.685	0.665	0.775	0.850	0.705	0.695	0.780	0.620	1.000	0.950	1.020
P %	0.135	0.120	0.165	0.170	0.120	0.125	0.135	0.140	0.210	0.180	0.160
N/P	21.700	19.420	10.970	11.240	16.080	16.800	13.410	15.070	7.140	11.440	11.190
Ca ppm	4926.000	3809.000	5620.000	4558.500	4873.000	5857.000	3935.000	8097.000	6990.000	7284.000	5560.000
Ca/Al	32.930	22.880	33.500	44.420	39.250	59.040	32.780	55.650	80.820	84.180	63.410
Mg ppm	1231.500	908.100	1482.000	1190.700	1170.500	1872.500	1015.500	1808.500	1764.000	2218.000	1663.000
S ppm	2694.500	1791.000	1898.000	1539.500	1497.000	1559.000	1619.500	1960.500	1883.500	1434.000	1428.000
Fe ppm	300.400	488.700	421.900	462.100	315.400	234.400	245.000	362.600	158.100	137.300	182.100
Mn ppm	1880.500	1549.000	1562.000	650.100	988.700	1629.500	1746.500	2002.000	904.800	1745.000	1081.000
Pb ppm	2.670	3.580	2.020	2.790	2.800	1.480	1.270	3.330	0.810	0.255	0.732
Al ppm	149.800	166.200	169.050	98.030	125.670	100.530	117.450	150.330	86.170	86.530	87.680
Toleranz-Indikationen der Bäume und des Waldes											
Aktive Mykorrhiza	13.600	18.200	23.700	16.000	7.250	49.800	11.500	15.700	29.500	38.400	96.000
Wurzelspitzen ohne Mykorrhiza	95.100	73.400	62.400	76.900	67.400	48.000	57.700	74.700	39.000	70.000	14.800
Wurzelspitzen mit Mykorrhiza	38.300	56.400	59.600	75.500	29.200	81.300	34.400	45.300	80.200	76.200	130.800
Tracheenverstopfungen %	44.060	34.900	34.990	37.620	33.640	19.800	13.860	44.220	8.560	2.170	6.400
Unkraut %	90.000	90.000	75.000	50.000	85.000	85.000	80.000	80.000	5.000	0.000	0.000
Baumsterben %	65.000	60.000	45.000	30.000	60.000	40.000	55.000	60.000	3.000	0.000	0.000

27 Parameter im Baumsterben eine physiologische Rolle, jeder jedoch mit einer anderen Wertigkeit. Für den Vergleich dieser Parameter und den eventuell vorhandenen Synergismus wären jedoch weitere recht ausführliche (auch experimentell kontrollierte) Untersuchungen notwendig. Die zusammengefassten Rechnungen mit diesen Parametern können trotzdem recht informativ sein. Auf diese Weise konnte man darauf schliessen, wie hoch der Degradierungsgrad der einzelnen Probeentnahmestellen ist und ob ein eindeutiger Zusammenhang zwischen Degradierungsgrad und Entfernung von den Luftverschmutzungsquellen festgestellt werden kann.

Zur Durchführung der multivarianten Statistikverfahren (Clusteranalyse, Faktoranalyse) wurden unsere Ausgangswerte zur normalen Zufallsvariable mit Erwartungswert 0 und Einheitsstreuung transformiert (LEGENDRE und LEGENDRE 1983, SOKAL und ROHLF 1969).

Der z_{ij} normierte Wert wurde nach folgendem Zusammenhang ermittelt:

$$z_{ij} = \frac{x_{ij} - \bar{x}_i}{s_i}, \quad i = 1, \dots, n; \quad j = 1, \dots, t$$

wobei x_{ij} der Merkmalswert Typ i in j -ter Probeentnahmestelle, \bar{x}_i der durchschnittliche Merkmalswert Typ i , also

$$\bar{x}_i = \sum_{j=1}^t x_{ij}/t, \quad$$

und s_i die Streuung

$$s_i = \left(\sum_{j=1}^t (x_{ij} - \bar{x}_i)^2 / (t-1) \right)^{1/2}$$

darstellen, wobei n die Anzahl der Probeentnahmestellen und t die Anzahl der gemessenen Merkmalswerte angeben.

Die Clusteranalyse ist ein multivariantes Statistikverfahren, mit deren Hilfe die Prüfobjekte aufgrund ihrer Ähnlichkeit oder Verschiedenheit objektiv gruppiert (ganz genau gesagt: in Klassen geteilt) werden können (ANDERBERG 1973, SNEATH und SOKAL 1973, PODANI 1980, SPATH 1980, ROMESBURG 1984), weshalb sie in unseren Auswertungsarbeiten zum Einsatz kam.

Der Abstand zwischen den einzelnen Probeentnahmestellen wurde nach der euklidischen Distanzfunktion angegeben. Der Abstand d_{jk} zwischen den j -ten und k -ten Probeentnahmestellen in den gemessenen Merkmalswerten gerechnet, wird folgendermassen ausgedrückt:

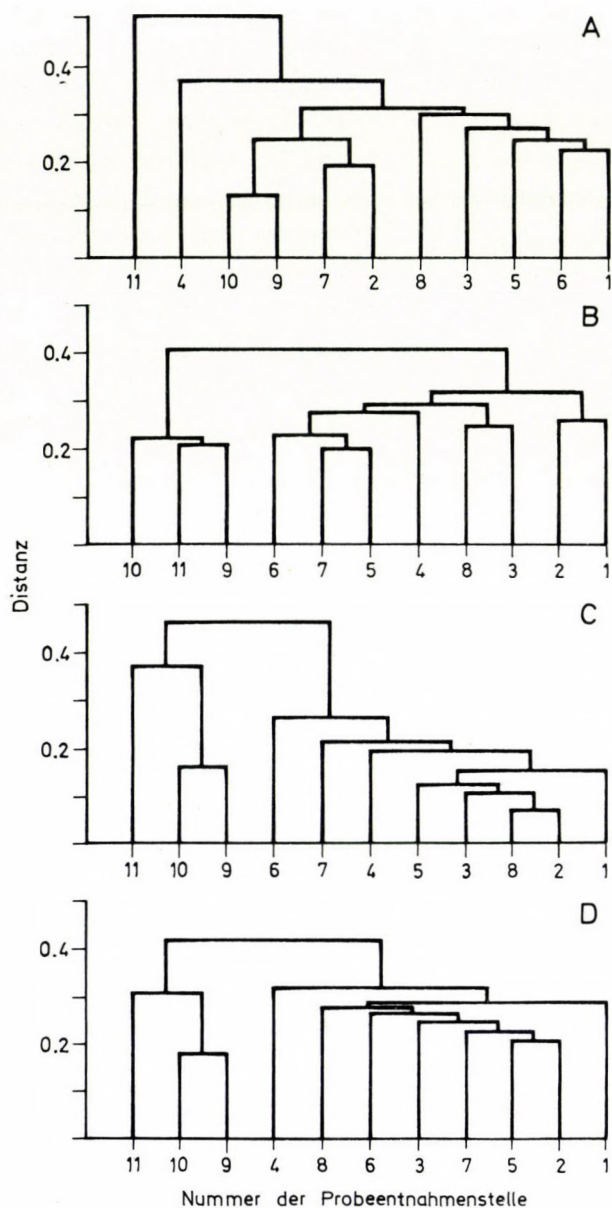


Abb. 2. Cluster-Diagramme aufgrund charakteristischer Daten über "Boden" (A), "Blatt" (B), "Baum-Wald" (C) und "Total" (D)

$$d_{jk} = \left[\sum_{i=1}^t (z_{ij} - z_{ik})^2 \right]^{1/2}$$

Von den Funktionsmethoden wurden die einfache und die Totalketten-Methode sowie die einfache und die Gruppenmittelwert-Methode verwendet (ORLÓCI 1978, PIELOU 1984). Sämtliche Methoden führten im Wesentlichen zu den gleichen Ergebnissen, weshalb die Cluster-Diagramme in Abbildung 2. nur die Ergebnisse der Totalketten-Methode zeigen.

Das aufgrund der Bodenmerkmale erhaltene Cluster-Diagramm lässt eindeutig feststellen, dass die Probeentnahmestellen Nr. 9 und 10 am meisten ähnlich sind. Der Grund dafür liegt darin, dass der genetische Bodentyp dieser zwei Gebiete der auf Quarzitschiefer entstandene saure, nicht podsolige braune Waldboden ist, während in den anderen Gebieten Parabraunerde zu finden ist. Der Boden des Kontrollwaldes Nr. 11 sondert sich auffällig ab und kann hinsichtlich der einzelnen Parameter auf jeden Fall als der günstigste beurteilt werden.

Die gesunden Kontrollen NR. 9, 10 und 11 weichen bezüglich der Merkmale "Blatt", "Baum-Wald" und "Gesamt" eindeutig von den industrienahen Probeentnahmestellen (Nr. 1-8) ab.

Die Faktoranalyse wurde bei der Auswertung deshalb eingesetzt, weil nach ihrem Ausgangspunkt die beobachteten Zufallsgrößen als lineare Funktion gewisser hypothetischer Zufallsvariablen ausgedrückt werden können. Somit stellt sie ein geeignetes Verfahren dar, um die zahlreichen korrelierten Zufallsvariablen durch wenige unkorrelierte Variable zu erklären. Diese hypothetischen Variablen werden Faktoren genannt. Aus den Lösungsvarianten der Faktoranalyse wurde von uns die Zentroid-Methode verwendet (JAHN und VAHLE 1968, LAWLEY und MAXWELL 1981, ÉLTETŐ et al. 1982). Bei der Zentroidanalyse wurde aus der Korrelationsmatrix der Ausgangswerte ausgegangen.

Auch in diesem Fall wurden die Rechnungen jeweils für die Bodenparameter, für den Mineralstoffgehalt der Blätter, für Parameter — durch welche der Gesundheitszustand der Bäume und der Wälder beurteilt wurde — sowie für die aufgeführten Parametergruppen dreierlei Typs gemeinsam durchgeführt (Ab. 3-4).

Es kann eindeutig festgestellt werden, dass bei Qualifizierung der Gebiete aufgrund der untersuchten Parameter, zwischen einer relativ schadefreien Gruppe (9, 10, 11) sowie einer geschädigten Gruppe (1-8) unter-

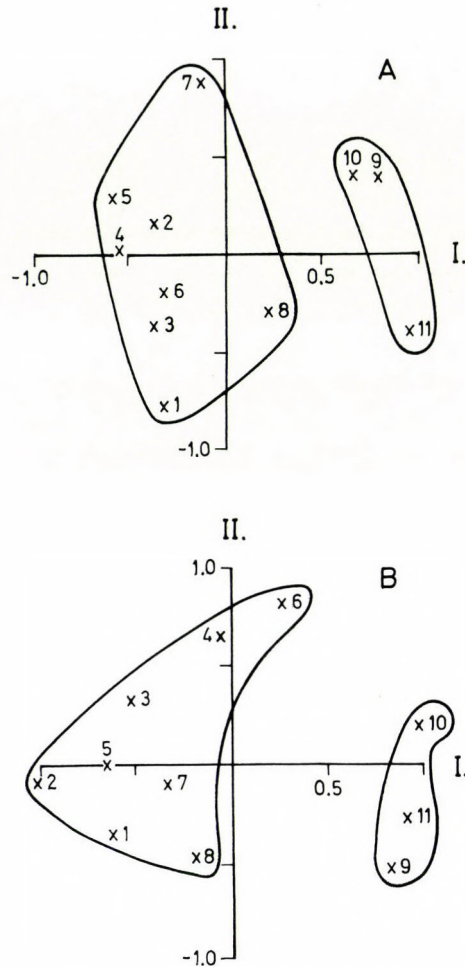


Abb. 3. Zentroides Diagramm aufgrund von bodenchemischen (A) und blattchemischen (B) Daten

schieden werden kann. Letztere Gruppe weist ebenfalls unterschiedliche Schädigungsgrade auf. So z.B. sind die Bestände der Probeentnahmestellen Nr. 4 (Tapolca) und 6 (Kazincbarcika: Ibolyás) weniger degradiert als die anderen Bestände. Dies zeigt auch die geringere prozentuale Absterbensrate der Bäume in diesen Gebieten.

Zum Abschluss wurde noch eine Auswertung durchgeführt, in welcher man für die Werte der 27 Parameter in der Tabelle 2. Rangnummern von 1 bis 11 einsetzte. Die 11 bedeutet in dieser Reihenfolge den günstigsten Wert hinsichtlich der gesünderen Ökologie des Baumes und die 1 den ungünstigsten.

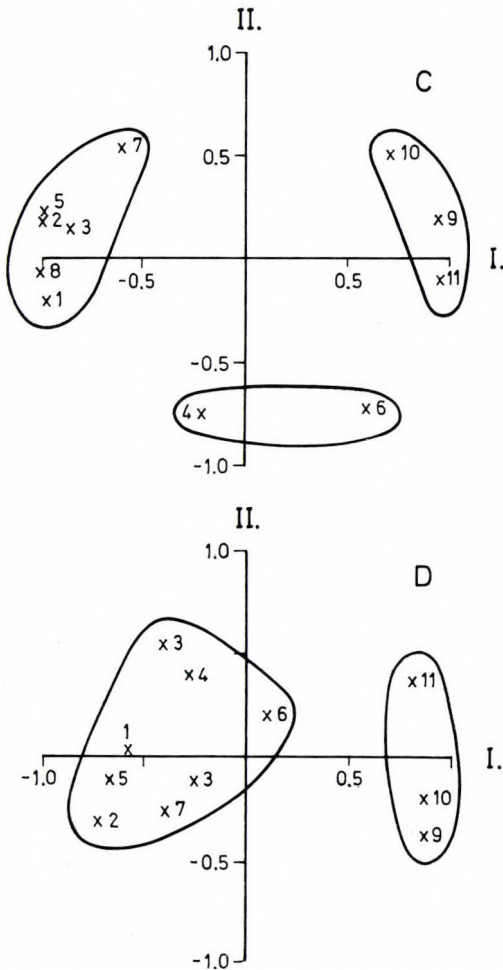


Abb. 4. Zentroides Diagramm aufgrund von Baum-Wald (C) sowie sämtlicher (Total) (D) Daten

Die Zahlen wurden vertikal addiert, womit wir kumulative Qualifizierungswerte (zwischen 80 und 260) erhielten, bei welchen die höheren einen günstigeren und die niedrigeren einen ungünstigeren Zustand beschreiben. Diese Werte wurden von uns Degradationsrangnummern genannt und in Abhängigkeit der km-Entfernung von den industriellen Emissionsquellen graphisch dargestellt (Abbildung 5).

Aus der Abbildung ist eindeutig ersichtlich, dass der ungünstigste Zustand für die zwei Musterwälder besteht, welche näher als 1 km zu den Emissionsquellen liegen. Die Situation der Musterstellen zwischen 2 bis

3 km ist kaum besser. Ein ebenfalls noch starker Degradationsgrad ist in den Musterstellen zwischen 4 bis 12 km zu finden.

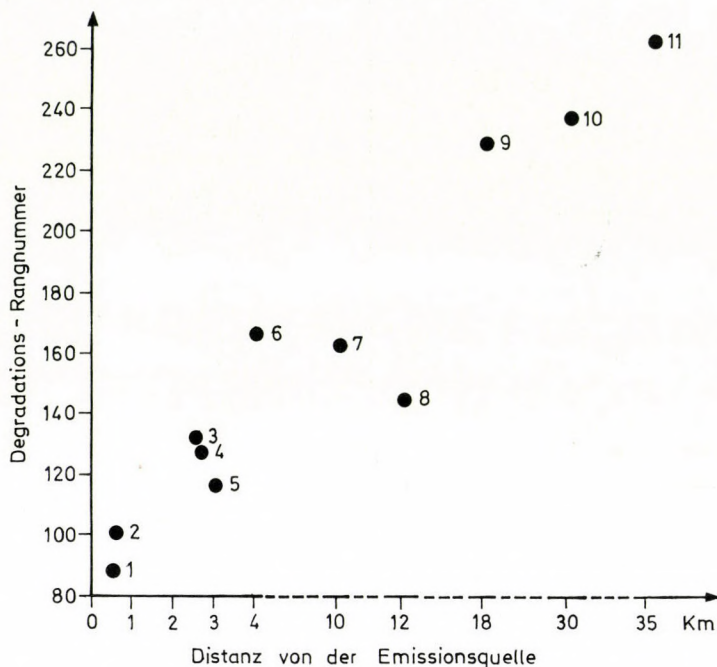


Abb. 5. Degradierungs-Rangnummer der einzelnen Probeentnahmestellen (1-11) und ihre Distanz von den industriellen Emissionsquellen

Die in 18-35 km Entfernung liegenden "Kontroll"-Bestände weisen demgegenüber hohe "Degradationsrangnummern" auf, und somit wird eindeutig bewiesen, dass durch die lokale industrielle Luftverschmutzung der Absterbevorgang der Bäume und die Störung der Waldstabilität in drastischem Masse beeinflusst sowie die Degradationsprozesse verstärkt werden.

LITERATUR

- Anderberg, M.R. (1973): Cluster Analysis for Applications. Academic Press, New York.
- Berki, I., Holes, L. (1988): Lokale industrielle Luftverschmutzung und Waldschäden in Nordungarn II. Mineralstoffgehalt des Bodens und der Blätter von Quercus petraea s.l. Acta Bot. Hung., 34: 25-37.
- Éltető, Ö., Meszéna, Gy., Ziermann, M. (1982): Stochastic Models and Methods (in Hungarian). Közg. és Jogi Könyvkiadó, Budapest.

- Holes, L., Berki, I. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn III. Gestaltung des Nebenwurzelwerkes und der Mykorrhiza. Beziehungen bei gesunden und kranken Bäumen. Acta Bot. Hung., 34: 39-49.
- Igmándy, Z., Béky, A., Pagony, H., Szontagh, P., Varga, F. (1986): The state of decay of sessile oak in Hungary in 1985 (in Hungarian). Az Erdő, 35: 255-259.
- Jahn, W., Vahle, H. (1986): Die Faktoranalyse und ihre Anwendung. Verl. die Wirtschaft, Berlin.
- Jakucs, P. (ed.), (1983): Ökologische Untersuchung des Gesundheitszustandes von Eichenbeständen in Ungarn (ungarisch). Mskr.
- Jakucs, P. (1988): Ecological approach of forest decay in Hungary. AMBIO, 17: 267-274.
- Jakucs, P., Mészáros, I., Papp, B.L., Tóth, J.A. (1986): Acidification of soil and decay of sessile oak in the "Síkfőkút Project" area (N-Hungary). Acta Bot. Hung., 32: 303-322.
- Jakucs, P., Babos, K. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn IV. Jahrringbreiten und Tracheenverstopfungen von gesunden und erkrankten *Quercus petraea* s.l. Stämmen. Acta Bot. Hung., 34: 51-64.
- Karl-Urban, B., Papke, H., Schimansky, Chr., Peters, K. (eds) (1987): Waldschäden. 2nd Ed. KFA. Jülich, Kopp OHG, Köln.
- Klein, R.M., Perkins, T.d. (1987): Cascade of causes and effects of forest decline. AMBIO, 16: 86-93.
- Lawley, D.N., Maxwell, A.E. (1971): Factor Analysis as a Statistical Method, 2nd ed., Butterworths, London.
- Legendre, L., Legendre, P. (1983): Numerical Ecology. Elsevier Sc. Publ. Comp., Amsterdam-Oxford-New York.
- McLaughlin, S.b. (1985): Effects of air pollution on forests. J. Air Poll. Contr. Assoc., 35: 512-534.
- Mészáros, I. (1984): Comparative chemical analysis of the soil, the root and the leaf in the decay of the sessile oak (in Hungarian), Az Erdő, 33: 367-369.
- Orlóci, L. (1978): Multivariate Analysis in Vegetation Research. W. Junk. The Hague.
- Pielou, E.C. (1984): The Interpretation of Ecological Data. J. Wiley and Sons, New York.
- Podani, J. (1980): SY-TAX: A Computer program package for ecological, coenological and taxonomical classification (in Hungarian). Abstracta Bot., 6: 1-158.
- Romesburg, H.C. (1984): Cluster Analysis for Researches. Lifetime Learning Publ., Belmont.
- Schütt, P. (ed.), (1984): Der Wald stirbt and Stress. Bertelsmann, München.
- Schütt, P., Cowling, E.B. (1985): Waldsterben, a general decline of forests in Central Europe: symptoms, developments and possible causes. Plant Disease, 89: 548-558.

- Smith, W.H. (1981): Air Pollution an Forests. Springer, New York Inc.
- Sneath, P.H.A., Sokal, R.R. (1973): Numerical Taxonomy. Freeman, San Francisco.
- Sokal, R.R., Rohlf, F.J. (1969): Biometry. The Principles and Practice of Statistics in Biological Research. Freeman, San Francisco.
- Späth, H. (1977): Cluster-Analyse-Algorithmen zur Objektklassifizierung und Datenreduktion, 2. Aufl., Oldenburg Verl., München-Wien.
- Ulrich, B., Mayer, R., Khanna, P.K. (1979): Deposition von Luftverunreinigungen und ihre Auswirkung in Waldökosystemen im Solling. Schriften Forstl. Fak. Univ. Göttingen, 58: 1-291.
- Ulrich, B., Pankrath, J. (eds), (1983): Effects of Accumulation of Air Pollutans in Forest Ecosystems. Reidel Publ. Comp., Hingham.
- Woodman, J.N., Cowling, E.b. (1987): Airborne chemicals and forest health. Environm. Sc. and Technol., 21: 120-126.

LOKALE INDUSTRIELLE EMISSION UND WALDSCHÄDEN IN NORDUNGARN II.
MINERALSTOFFGEHALT DES BODENS UND DER BLÄTTER VON QUERCUS PETRAEA S.L.

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Changes in the element content of leaves of healthy and diseased sessile oak trees and of the soil caused by the industrial air pollution have been studied in different distance from the industrial area of the Sajó river valley, in North-Hungary. As a consequence of the air pollution, near the industrial area the soil has become more acid than in the control stands. The concentration of the NO_3 and the easily soluble Al has increased while the Ca and Mg content has dropped. Approaching the emission sources the content of N, S, Al, Fe, and Mn of the leaves increases, while the concentration of some important macroelements (P, K, Ca, Mg) decreases. These changes notably modified the rates of elements in the leaves of sessile oak trees as well as in the soil. The changes of chemical composition, which are disadvantageous from ecophysiological point of view, may play a role in stronger and quicker destruction of the forests exposed to local industrial air pollution.

EINFÜHRUNG

In der europäischen und nordamerikanischen Fachliteratur bezüglich der Aufklärung von Ursachen für neuartige Erkrankungs- und Absterbevorgänge der Bäume, werden Forschungsarbeiten bevorzugt, bei welchen die veränderten Mineralstoffgehalte der geschädigten Bäume und der Böden im Mittelpunkt stehen. Die überwiegende Mehrheit der Fachartikel beschäftigt sich mit den Bäumen der Nadelwälder (HÜTTL und ZÖTTL 1985), deren Schädigung in Europa und Amerika wirtschaftlich bedeutender ist. Darüber hinaus sind in den genannten Gebieten Wälder mit diesen Baumarten dominierend (ZÖTTL und MIES 1983). Über Untersuchungen des Mineralstoffgehaltes von Laubbäumen berichten BREDOV et al. (1986) sowie GLAVAČ (1987).

Die Prüfungen der Schadwirkungen von Luftschadstoffen auf Bäume werden teils direkt im Untersuchungsgebiet, teils in Klimakammern durch Simulationsmodelle durchgeführt (WOODMANN und COWLING 1987). Die ver-

schiedenen Methoden stimmen jedoch darin überein, dass die neuartigen, sich rasch verbreitenden Waldschäden und das Baumsterben auch durch die Veränderung der Mineralstoffgehalte des Bodens sowie der Assimilationsorgane der Bäume gekennzeichnet werden. Die im Boden ablaufenden Wandlungen zeigen sich auch in der selektiven Ionenaufnahme der Bäume und dadurch auch im veränderten Mineralstoffgehalt der Laubblätter.

Die Wirkung der Luftschadstoffe (SO_2 , NO_x), die sich über grosse Flächen verbreiten, kann durch die Immision im direkten Umkreis der Industriegebiete verstärkt werden. 1987 wurde von uns zum Nachweis der lokalen Wirkung von emittierten Luftschadstoffen (SO_2 , nitrose Gase, Chlor, Schwermetalle) eines grossen Industriegebietes in Nordungarn (im Sajó-Tal) ein komplexes Untersuchungsprogramm durchgeführt. In diesem Programm wurden mehrere abiotische und biotische Parameter zur Aufklärung des Baumsterbens gleichzeitig untersucht, wobei die Proben von Untersuchungsstellen entnommen wurden, die von den Emissionsquellen kontinuierlich entfernter lagen (JAKUCS et al. 1988, HOLES und BERKI 1988, JAKUCS und BABOS 1988).

Wir hielten den Mineralstoffgehalt der Böden und der Blätter der Baume deshalb für wichtig, weil nach FIEDLER et al. (1973) die Traubeneiche unter den Eichensorten die grössten Nährelementansprüche besitzt, und auf die eventuell auftretende Veränderung des Nährelementgehaltes infolge Luftverschmutzung empfindlich reagiert.

In der vorliegenden Arbeit werden die Untersuchungsergebnisse der chemischen Analysen von Boden und Blättern zusammengefasst.

UNTERSUCHUNGSMATERIAL UND METHODE

Das Untersuchungsgebiet und die wichtigsten Daten der geprüften Waldbestände sind in der Veröffentlichung von JAKUCS et al. (1988) beschrieben. Zwischen 13. und 17. Juli 1987 wurden in einem 0,5 bis 12 km breiten Umkreis der industriellen Emissionsquellen bei 8 Waldbeständen Proben entnommen. Das Baumsterben in diesem Gebiet ist im Vergleich mit dem Landesdurchschnitt wesentlich stärker. Als Kontrolle wurden zur gleichen Zeit bei 3 Beständen, welche 18 bis 35 km entfernt vom Industriegebiet liegen, ebenfalls Proben entnommen. Bei der Auswertung wurden jedoch auch Untersuchungsergebnisse von 5 Kontrollwäldern verwendet, welche in Westungarn und entfernt jeglicher industrieller Emission stehen. Von BREDOV et al. (1986) wird ebenfalls diese Methode vorgeschlagen, nach welcher die Proben industrienaher sowie entfernter, gesunder Bestände zum Nachweis der Wirkung von lokaler Luftverschmutzung geeignet sind.

Bei den untersuchten Beständen wurden aus drei genetischen Bodenhorizonten Proben entnommen (A_1 = 0–10 cm; AB = 10–30 cm; B_1 = 30–50 cm). Anschliessend wurden die Bäume über den Probeentnahmestellen gefällt und

aus dem Laub eine Mischprobe entnommen (obere-mittlere-untere Schicht). In den industrienahen Gebieten, wo die gesunden und kranken Bäume nebeneinander standen, wurden die Proben je Baumpaar entnommen. In dieser Arbeit werden jedoch bevorzugt nur die Daten der gesunden Bäume gezeigt, weil die Wälder der Kontrollgebiete nur vereinzelt kranke Bäume enthielten.

Untersuchungsparameter und -elemente werden in den Tabellen 1. und 2. dargestellt.

Die Boden- und Blattanalysen wurden in Untersuchungsstationen für Pflanzenschutz und Agrochemie in den Bezirken Borsod und Hajdú-Bihar durchgeführt. Der hydrolytische Säuregrad (y_1) bedeutet die potentielle Azidität, welche mit einer 0.5 Mol/l $\text{Ca}(\text{CH}_3\text{COO})_2$ -Lösung (pH-Wert = 8.0) titriert wird. Unter austauschbarer Azidität (y_2) versteht man den Säuregrad, welcher nach der Extraktion mittels einer 1 mol/l KCl-Lösung titriert werden kann.

Die Extraktion von NO_3^- -N, NH_4^+ -N, SO_4^{2-} -S und Mg aus dem Boden erfolgte mittels 1 Mol/l KCl-Lösung, zur Auslösung von P_2O_5 , K_2O und Na diente Ammoniumlactat-Lösung (AL-Lösung). Die übrigen Elemente der Tabelle 1. wurden durch EDTA-Extraktion aufgeschlossen. Das Extraktionsmittel enthielt 0.05 Mol/l EDTA und 0.01 Mol/l KCl.

Zur Bestimmung des Gehaltes an N, P, K und Na in den Blattproben wurde das Untersuchungsmaterial mit einem Gemisch von konz. H_2SO_4 + H_2O_2 aufgeschlossen, bei den anderen Elementen verwendete man dazu ein Gemisch aus konz. HNO_3 und H_2O_2 . Die Messungen wurden bei Humus, NO_3^- -N, NH_4^+ -N, SO_4^{2-} -S und P_2O_5 mit einem Photometer Typ OL 603, bei K_2O und Na mit einem Flammphotometer Typ OM.SZÖV OE 85 und bei den übrigen Elementen mit einem Spektrometer UV-25 Labtest ICP durchgeführt.

Ergebnisse der Bodenanalyse (Tabelle 1)

Bei den 16 Traubeneichenbeständen findet man in 12 Fällen auf den tertiären Ablagerungen entstandene Parabraunerde und in 4 Fällen auf dem Schiefer entstandener, saurerer, nicht podsoliger brauner Waldboden. Von den untersuchten 3 Bodenhorizonten ist hinsichtlich der Nährstoffaufnahme der Bäume der 10–30 cm tief liegende AB-Horizont am wichtigsten, in diesem Horizont befindet sich nämlich der grösste Teil des Nebenwurzelwerkes der Traubeneiche. Dementsprechend werden in der Tabelle 1 sowie in den Abbildungen 1 bis 4 die Durchschnittswerte des Mineralstoffgehaltes in diesem Horizont dargestellt.

Nachfolgend werden vor allem Bodenparameter gewertet, welche aufgrund der erhlatenen Ergebnisse in dem durch lokale industrielle Luftverschmutzung verstärkten Prozess des Eichensterbens vermutlich eine Rolle spielen.

Aus Tabelle 1 ist ersichtlich, dass der Boden der untersuchten Bestände stark sauer ist. Es ist gleichzeitig ebenfalls zu sehen, dass die zwei verschiedenen Bodensauergrad (y_1 und y_2) und die unterschiedlichen pH-Werte (in H_2O und in KCl gemessen) im Vergleich mit den Kontrollbeständen eindeutig auf die Versauerung der Böden industrienaher Bestände hinweisen.

Tabelle 1

Durchschnittswerte der Bodenanalysen bei Traubeneichenbeständen (im Boden-
horizont von 10 bis 30 cm) bei gesunden Bäumen

	Industriennahe Bestände (n = 7)		Kontroll Bestände (n = 7)	
	\bar{x}	s	\bar{x}	s
pH _(H₂O)	3.91	± 0.28	4.47	± 0.50
pH _(KCl)	3.24	± 0.17	3.89	± 0.67
Y ₁	42.16	± 14.14	24.39	± 9.60
Y ₂	28.84	± 15.74	17.30	± 4.30
Humus %	1.67	± 0.32	1.92	± 1.08
NO ₃ ⁻ -Nppm	7.76	± 7.28	0.81	± 0.45
NH ₄ ⁺ -Nppm	4.09	± 1.56	12.92	± 8.48
P ₂ O ₅ ppm	42.14	± 64.96	17.57	± 22.66
K ₂ O ppm	143.3	± 56.96	116.1	± 33.09
SO ₄ ²⁻ -Sppm	22.54	± 13.61	17.38	± 10.16
Ca ppm	254.9	± 218.9	425.6	± 500.5
Mg ppm	68.43	± 49.98	123.1	± 89.28
Mn ppm	343	± 203.3	492.8	± 370.4
Na ppm	26.57	± 11.16	29.70	± 15.32
Fe ppm	481.1	± 204.6	444	± 137.1
Al ppm	843	± 359.1	494.7	± 246.6
Zn ppm	2.20	± 0.98	2.29	± 1.19
Cu ppm	2.06	± 1.17	1.85	± 0.70
B ppm	0.806	± 0.25	0.734	± 0.45
Mo ppm	0.130	± 0.09	0.039	± 0.03
Ni ppm	1.68	± 1.40	1.7	± 0.88
Li ppm	0.089	± 0.06	0.058	± 0.06
Co ppm	5.77	± 2.44	5.68	± 2.59
Cr ppm	0.130	± 0.08	0.186	± 0.10
Pb ppm	10.97	± 1.96	11.02	± 2.86
Cd ppm	0.056	± 0.02	0.056	± 0.03
Ca/Al	0.29	± 0.26	0.86	± 0.59

Der $\text{pH}_{(\text{KCl})}$ -Wert des AB-Horizontes bei kranken Eichenbeständen in industrienahen Gebieten beträgt durchschnittlich nur 3.25! Die Versauerung durch industrielle Luftverschmutzung wird durch den grösseren Säuregrad des Bodens bei industrienahen Beständen ebenfalls unterstützt. Bei 8 Kontrollgebieten findet man nämlich in 4 Fällen einen saueren, nicht podsoligen Waldboden, welcher auch ursprünglich, aus seiner Genetik her stark sauer war. Die Industrienahen Bestände sind jedoch in sämtlichen Fällen auf Parabraunerde zu finden welche ursprünglich nicht so sauer hätten sein dürfen, wie der saure, nicht podsolige braune Waldboden.

Durch die Mitarbeiter unseres Lehrstuhls wurden im Eichenbestand von "Síkfölkút Project" nach 10 Jahren erneut mehrere Bodenprofile untersucht und die Ergebnisse bewiesen die zunehmende Versauerung des Bodens (BERKI 1987). In den nahe liegenden Mátra- und Zemplén-Gebirgen wurde vor 20 Jahren der unter den ähnlichen Eichen-Zerreichen Beständen vorhandene Bodentyp geprüft. In keinem der Bodenprofile war der Säuregrad so hoch, wie die Werte, welche von uns 1987 im Umkreis des Industriegebietes Sajó-Tal gemessen wurden (KOVÁCS 1975, SIMON 1977).

Nach Angaben von STEFANOVITS (1986) ist der titrierbare Säuregrad (y_1 und y_2) der Waldböden in Ungarn (inklusive der Böden von derzeitigen Waldbeständen) innerhalb von 25 Jahren durchschnittlich auf den 2 bis 3-fachen Wert gestiegen.

Es kann also festgestellt werden, dass die starke Versauerung der Parabraunerde bei den Eichenbeständen in der Nähe vom Industriegebiet Sajó-Tal und die verstärkte Luftschadstoffemission (SO_2 , NO_x) dieser Betriebe vermutlich im Zusammenhang stehen.

Im Zusammenhang mit den Bodenreaktionsverhältnissen kann auch die Veränderung des Gehaltes an leicht löslichem Ca und Al gewertet werden. Die Absolutmengen dieser zwei Elemente und besonders deren Mengenverhältnis (Ca/Al-Verhältnis) sind auf die pH-Verhältnisse des Bodens charakteristisch (s. ULRICH und PANKRATH).

In der ganzen Region enthält der Boden der Kontrollgebiete entsprechend dem niedrigeren pH-Wert durchschnittlich 425,6 ppm Ca, im gleichen Bodenhorizont der industrienahen Gebiete sind jedoch durchschnittlich nur noch 254,8 ppm Ca zu finden. Im Boden der industrienahen Gebiete – aufgrund des niedrigeren pH-Wertes im Vergleich mit den Kontrollgebieten – beträgt der lösliche Al-Gehalt beinahe 50% mehr (843 ppm), als im Boden der Kontrollgebiete (495 ppm). Dementsprechend beträgt das Ca/Al-Verhältnis im Boden der industrienahen Gebiete nur 34% (0.29) des Ca/Al-Verhältnisses im Boden der Kontrollgebiete (0.86).

Im Boden der industrienahen Eichenbestände wurde nur ein Drittel der in den Kontrollböden gemessenen NH_4^+ -Konzentration ermittelt. Der NO_3^- -Wert war demgegenüber fast 10-fach höher in den Böden der industrienahen Bestände, als bei der Kontrolle. Dieser NO_3^- -Überschuss kann zum Teil aus den nitrosen Gasen der nahe liegenden Fabriken stammen. Auf ähnliche Weise bilden emittierter SO_2 -Überschuss und Luftfeuchtigkeit eine Säure, durch welche der SO_4^{2-} -Gehalt im Boden der industrienahen Eichenbestände im Vergleich mit den Kontrollgebieten zunimmt.

Der Gehalt an leicht löslichem Mg (dem Ca-Gehalt ähnlich) beträgt im Boden der industrienahen Eichenbestände etwa die Hälfte (68.4 ppm) des Durchschnittes im Kontrollboden (123.1 ppm). Bei den Untersuchungen der Böden von kranken und gesunden Nadelbeständen in Süddeutschland wurde ebenfalls festgestellt, dass die Menge des austauschbaren Mg und Ca im Boden der gesunden Wälder wesentlich grösser ist, als bei den kranken Wäldern (ZÖTTL und MIES 1983).

Ergebnisse der Blattanalyse (Tabelle 2)

Bezüglich des Mineralstoffgehaltes der Blätter gibt es gewisse Unterschiede zwischen den Eichenbeständen nahe des Industriegebietes Sajó-Tal und entfernter liegenderen Gebieten. Der N-Gehalt der Blätter in den industrienahen Beständen liegt kaum höher, als in den Kontrollbeständen. Dies beweist, dass trotz der verstärkten atmosphärischen N-Belastung im Umkreis der Betriebe der N-Gehalt der Blätter nur mässig zunahm. Nach Untersuchungen in Süddeutschland wurde bei Nadelbäumen trotz der während Jahrzehnte verstärkten Emission kein Zunahme des N-Gehaltes beobachtet (HÜTTL und ZÖTTL 1985, ZÖTTL und HÜTTL 1985).

In den Blättern der industrienahen Traubeneichen beträgt der durchschnittliche P-Gehalt 0.146% und der Durchschnittswert der Kontrollen 0.204% (Abb. 1). Der industrienahe P-Durchschnittswert ist nicht nur im Vergleich mit dem Kontrollwert gering, sondern auch in absolutem Sinn. Durch Versuche wurde bewiesen, dass die Traubeneiche die grösste Holzproduktion bei einem 0.22%-igen P-Gehalt der Blätter erreicht (NEWMANN und CARLISLE 1969).

In den industrienahen Gebieten vermindert sich in den Blättern auch der K-Gehalt (Abb. 2). Nach 20 Jahren erneut durchgeführte Nadelblattanalysen süddeutscher Nadelwälder zeigten, dass innerhalb von 2 Jahrzehnten der K-Gehalt der Nadelbäume stark abnahm. Die Verfasser halten den K-Mangel für eine der Ursachen für Schadsymptome (ZÖTTL und HÜTTL 1985).

Tabelle 2

Durchschnittswerte des Mineralstoffgehaltes der Blätter von Traubeneichen
(bezogen auf die Trockensubstanz), bei gesunden Bäumen

	Industrienaher Bestand (n = 8)		Kontroll Bestände (n = 8)	
	\bar{x}	s	\bar{x}	s
N %	2.105	± 0.22	1.89	± 0.23
P %	0.146	± 0.02	0.204	± 0.02
K %	0.768	± 0.11	1.09	± 0.11
S ppm	1710.0	± 234.5	1310.0	± 208.7
Ca ppm	5520.0	± 1304.3	6966.0	± 1008.7
Mg ppm	1312.0	± 346.3	1685.0	± 326.7
Mn ppm	1834.0	± 434.7	1399.0	± 701.3
Na ppm	312.0	± 39.72	262.0	± 67.46
Fe ppm	375.4	± 156.2	155.2	± 22.52
Al ppm	140.0	± 28.85	85.4	± 5.69
Zn ppm	18.98	± 1.78	16.85	± 3.21
Cu ppm	8.21	± 1.02	7.55	± 1.27
B ppm	29.66	± 5.42	19.93	± 4.60
Mo ppm	0.25	± 0.51	0.118	± 0.08
Ni ppm	7.56	± 9.35	4.58	± 1.79
Li ppm	0.31	± 0.08	0.064	± 0.06
Co ppm	0.433	± 0.37	0.171	± 0.24
Cr ppm	10.08	± 22.24	2.69	± 1.64
Hg ppm	7.71	± 2.37	5.59	± 2.58
Pb ppm	2.09	± 0.85	0.643	± 0.20
Cd ppm	0.162	± 0.08	0.138	± 0.06
N/P	15.43	± 4.35	9.38	± 1.49
N/K	2.81	± 0.63	1.63	± 0.45
Ca/Al	41.11	± 13.12	81.57	± 10.6

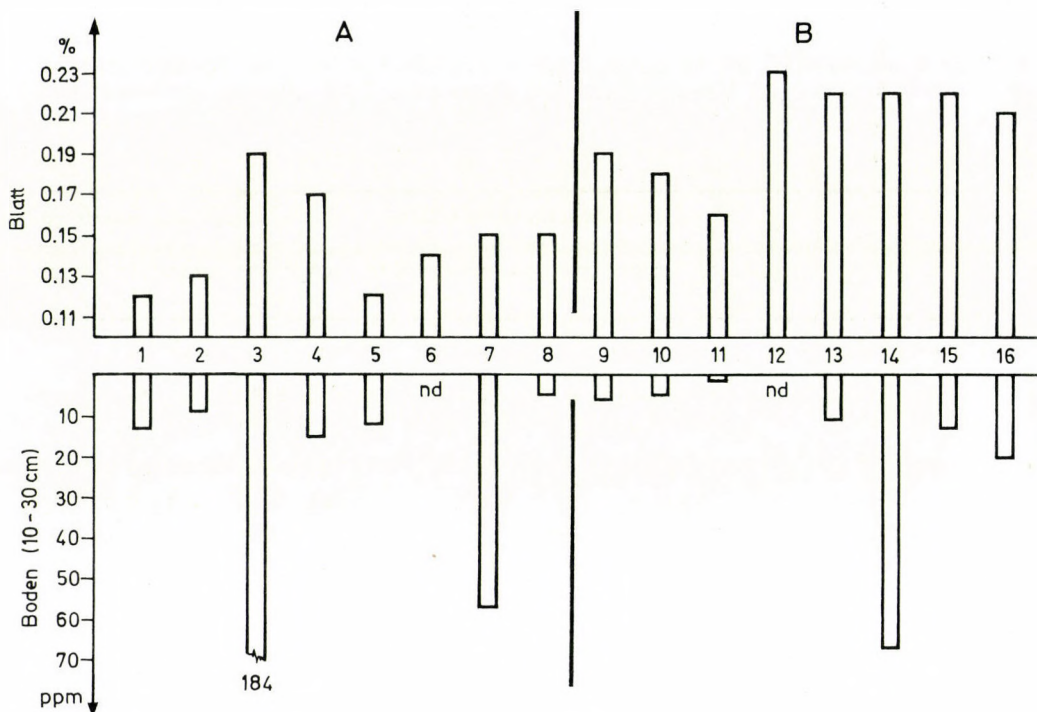


Abb. 1. P-Gehalt der untersuchten Traubeneichenbestände. Die einzelnen Bestände wurden in Reihenfolge der zunehmenden Entfernung vom Industriegebiet von links nach rechts dargestellt. A = Industrienähe Bestände. B = Kontroll-Bestände. 1 = Berente, 2 = Sajóbáony, 3 = Radostyán, 4 = Tapolca, 5 = Sajóivánka, 6 = Kazincbarcika, 7 = Putnok, 8 = Dédestapolcsány, 9 = Nagyvisnyó, 10 = Répáshuta, 11 = Trizs, 12 = Horvátút, 13 = Sopron, 14 = Bőszénfa, 15 = Kőszeg, 16 = Nagypáli

Aufgrund unserer Ergebnisse kann also festgestellt werden, dass in den industrienahen Gebieten der N-Gehalt der Blätter zwar mässig zunahm, der P- und K-Gehalt verminderte sich jedoch stark. Als Endergebniss dieser zwei entgegengesetzten Vorgänge ist in den Blättern der industrienahen Bestände ein bedeutender Zuwachs der N/P und N/K Verhältnisse zu beobachten (Tabelle 2).

Der kleinere P- und K-Gehalt der Blätter der industrienahen Bestände kann durch Fehlen dieser Elemente im Boden nicht erklärt werden. Das Vorkommen dieser Elemente im Boden industrienaher Bestände ist nämlich mindestens so gross, wie im Boden der Kontrollgebiete (Tabelle 1, Abb. 1 und 2).

In den Studien zur Nährstoffaufnahme der Bäume wird oft erwähnt, dass die P-Aufnahme der Wurzeln durch die symbiotischen Mykorrhiza-Pilze be-

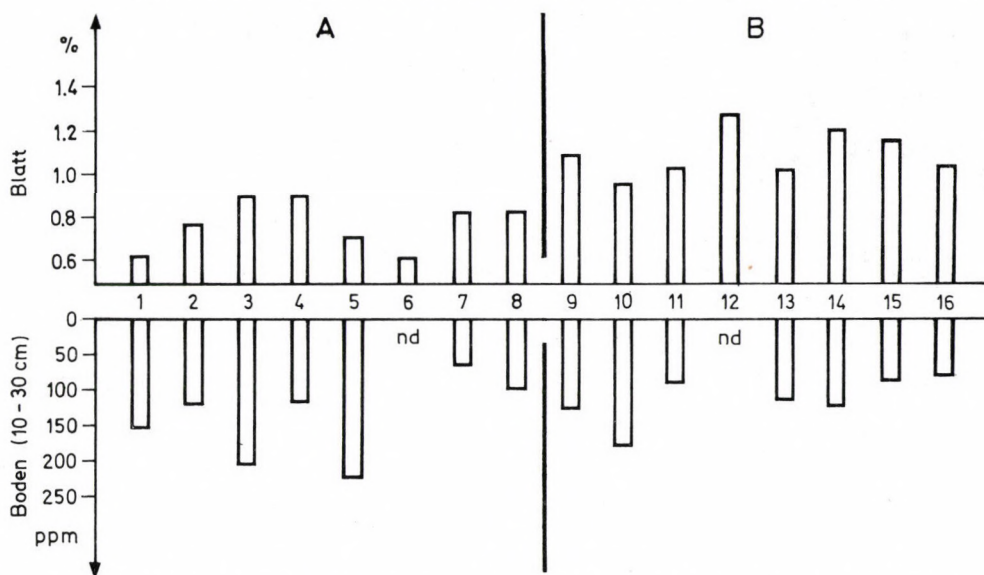


Abb. 2. K-Gehalt der untersuchten Traubeneichenbestände. (A, B und 1-16 s. Abb. 1.)

günstigt wird (MEYER 1962, AGERER et al. 1986). Auf den Wurzelspitzen der Traubeneichenbestände in der Nähe des Industriegebietes Sajó-Tal zeigen die Mykorrhiza-Beziehungen im Vergleich mit den Kontrollbeständen eine Degradation (HOLES und BERKI 1988). Aufgrund dieser Erscheinung ist anzunehmen, dass der niedrigere P-Gehalt der Blätter dieser Bestände auch mit der industrienahen Schädigung der Mykorrhiza-Beziehungen des Wurzelwerkes im Zusammenhang steht.

In den Blättern der zum Sajó-Tal nahe liegenden Bestände ist auch der Gehalt an Ca und Mg niedriger, als in den Kontrollgebieten (Tabelle 2).

Den bisher erwähnten Elementen gegenüber findet man jedoch in den Blättern der industrienahen Gebiete mehr S, Al, Mn und Fe (Tabelle 2, Abbildungen 3. und 4.). Von diesen Elementen kann ehestens nur der Al-Überschuss der Blätter mit dem erhöhten Al-Gehalt des Bodens im industrienahen Gebiet erklärt werden. Der Boden der industrienahen Bestände enthält nämlich nicht mehr Mn und Fe, als der Boden der Kontrollgebiete. Diese Tendenzen weisen vermutlich auf die selektive Elementenaufnahme der in ihrer Vitalität schwächer werdenden Bäume sowie auf den verstärkten Einbau toxischer Schwermetalle hin. Das Ca/Al-Verhältnis der Blätter in den Kontrollbeständen ist um das zweifache grösser, als in den industrienahen Gebieten. Die ungünstigen Wirkungen des Aluminiums auf die Pflanzen sind

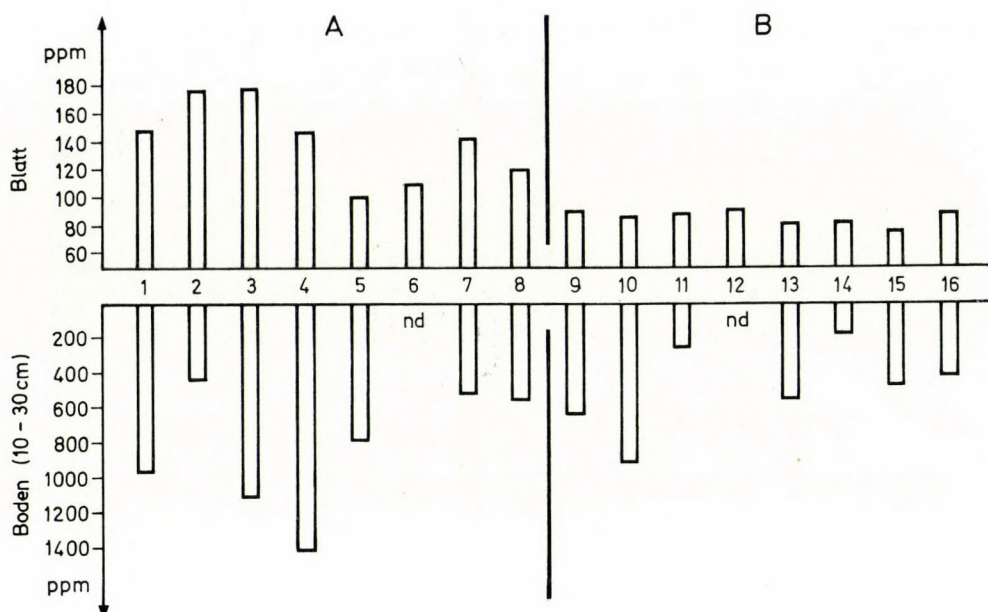


Abb. 3. Al-Gehalt der untersuchten Traubeneichenbestände. (A, B, und 1-16 s. Abb. 1.)

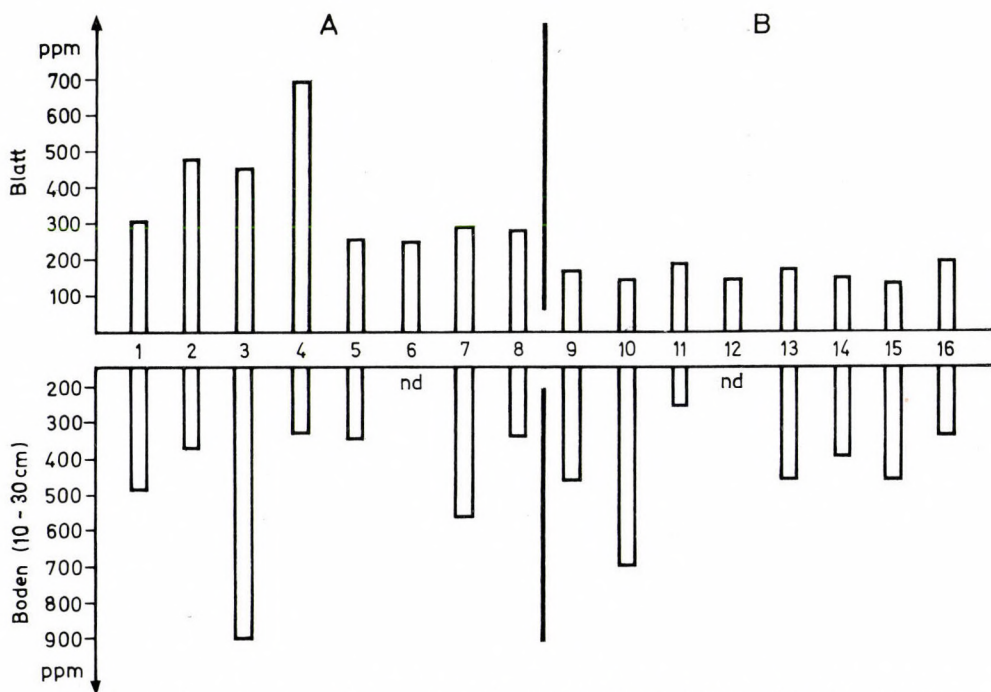


Abb. 4. Fe-Gehalt der untersuchten Traubeneichenbestände. (A, B und 1-16 s. Abb. 1.)

allgemein bekannt. Die übertriebene Aufnahme des Aluminiums wird z.B. vom hohen N- und Fe-Gehalt und vom geringen Mg- und Cu-Gehalt begleitet (MENDEL 1976).

In Ungarn wurden früher schon mehrmals bei Traubeneichen Blattanalysen durchgeführt (JÁRÓ und HORVÁTH 1962, TÖLGYESI 1965, 1969, PAPP 1985). Werden die Ergebnisse der Blattanalysen der von uns untersuchten 16 Wälder mit den Ergebnissen der vor 20 bis 25 Jahren durchgeführten Blattanalysen von anderen Traubeneichenbeständen im Land verglichen (TÖLGYESI 1965, 1969), so können folgende Feststellungen getroffen werden: Im Vergleich mit den Ca-Durchschnittswerten vor 20 Jahren (9500 ppm) nahm der Ca-Gehalt der Blätter ab, im Vergleich zu dem früheren Mn-Gehalt (564 ppm) nahm der Mn-Wert in sämtlichen von uns untersuchten Beständen zu. Der vor 20 Jahren ermittelte P-Gehalt (0.18%) ist grösser, als der P-Gehalt der Blätter in den industrienahen Beständen 1987, er ist jedoch etwas kleiner, als der Durchschnittswert der Kontrollen. Der Fe-Gehalt der Blätter in den Kontrollbeständen änderte sich in den 20 Jahren nicht.

Von BERGMANN (1983) wurden bezüglich der Traubeneichen Grenzwerte für Nährelemente festgelegt. Vergleicht man die Ergebnisse unserer Blattanalysen mit den oben erwähnten Grenzwerten, so kann festgestellt werden, dass der P-, K- und Mg-Gehalt der Blätter bei den Kontrollbeständen in dem von BERGMANN angegebenen Intervall liegt. Die gleichen Werte der industrienahen Gebiete erreichen jedoch nicht einmal den unteren Grenzwert!

Die Blätter der industrienahen Traubeneichenbestände enthalten im Vergleich zur Kontrolle auch von solchen Schwermetallen höhere Anteile, welche eigentlich hier in der Regel nur in sehr kleinen Mengen vorkommen (Co, Cd, Li, Hg, Pb — Tabelle 2). Der Überschuss kann einerseits aus der lokalen Verschmutzung und andererseits aus den löslichen Formen, welche in dem versauerten Boden in grösseren Mengen vorhanden sind, abgeleitet werden.

LITERATUR

- Agerer, R., Brand, F., Gronbach, E. (1986): Die exakte Kenntnis der Ektomycorrhizen als Voraussetzung für Feinwurzeluntersuchungen im Zusammenhang mit dem Waldsterben. Allg. Forst. Zschr., 20: 479-503.
- Bergmann, W. (1983): Ernährungsstörungen bei Kulturpflanzen: Entstehung und Diagnose. Gustav Fischer Verlag, Jena.
- Berki, I. (1987): Veränderungen einiger chemischen Parameter des Bodens innerhalb von 10 Jahren in der Parabraunerde beim "Síkfőkút Project". Mscr.

- Bredow, B., Buggert, A., Eckhoff, A., Hollstein, B., Neumann, M., Schindel, R., Zech, S., Glavač, V. (1986): Vergleichende Untersuchung der Boden-, Wurzel- und Blatt-Mineralstoffgehalte von Bäumen verschiedener Schadstufen in einem immissionsbelasteten Altbuchenbestand. Allg. Forst. Zschr., 22: 551–554.
- Fiedler, H.J., Nebe, W., Hoffmann, F. (1973): Forstliche Pflanzenernährung und Düngung. Gustav Fischer Verlag, Jena.
- Glavač, V. (1987): Calcium-, Magnesium-, Kalium- und Zink-Gehalte in Blättern eines immissionsgeschädigten Rendzina-Buchenwaldes. Allg. Forst. Zschr., 12: 303–305.
- Holes, L., Berki, I. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn III. Gestaltung des Nebenwurzelwerkes und der Mykorrhiza-Verhältnisse bei gesunden und kranken Bäumen. Acta Bot. Hung., 34: 39–49.
- Hüttl, R.F., Zöttl, H.W. (1985): Ernährungszustand von Tannenbeständen in Süddeutschland – ein historischer Vergleich. Allg. Forst. Zschr., 38: 1011–1013.
- Jakucs, P., Babos, K. (1988). Lokale industrielle Emission und Waldschäden in Nordungarn IV. Jahrringbreiten und Tracheenverstopfungen von gesunden und erkrankten Quercus petraea s.l. Stämmen. Acta Bot. Hung., 34: 51–64.
- Jakucs, P., Berki, I., Holes, L., Tóthmérész, B. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn I. Problemstellung, Ausgangshypothese und zusammenfassende Wertung. Acta Bot. Hung., 34: 11–24.
- Járó, Z., Horváth, E. (1962): Die periodischen und mengenmässigen Änderungen einiger Nährstoffe in den Blättern der Laubbäume. Hung. For. Sc. Rev., Budapest.
- Kovács, M. (1975): Beziehung zwischen Vegetation und Boden. Die Bodenverhältnisse der Waldgesellschaften des Mátragebirges. Akad. Kiadó, Budapest.
- Mengel, K. (1972): Ernährung und Stoffwechsel der Pflanze. Gustav Fischer Verlag, Jena.
- Meyer, F.H. (1962): Die Buchen- und Fichtenmykorrhiza in verschiedenen Böden, ihre Beeinflussung durch Mineraldünger sowie für die Mykorrhizabildung wichtige Faktoren. Mitt. Bundesforschungsanst. Forst – Holzwirtsch., 54: 1–73.
- Newnham, R.M., Carlisle, A. (1969). The nitrogen and phosphorus nutrition of seedling of Quercus robur L. and Q. petraea (Mattuschka) Liebl. J. Ecol., 57: 271–284.
- Papp, B.L. (1985): Nutrient content of woody plants. In Jakucs, P. (ed.): Ecology of an Oak Forest in Hungary, Results of Síkfőkút Project 1. Akad. Kiadó, Budapest, p. 321–348.
- Simon, T. (1977): Vegetationsuntersuchungen im Zempléner Gebirge. Akad. Kiadó, Budapest.
- Stefanovits, P. (1986): Einige neuere Angaben zur Versauerung der Böden (ungarisch). Magyar Tudom., 11: 339–341.
- Tölgyesi, Gy. (1965): Angaben zum Ca-, P-, Fe-, Mn-, Zn- und Cu-Gehalt von Bäumen und Sträuchern (ungarisch). Az Erdő, 14: 275–281.

- Tölgyesi, Gy. (1969): Mikroelementengehalt der Pflanze und dessen landwirtschaftliche Beziehungen (ungarisch). Mezőgazd. Kiadó, Budapest.
- Ulrich, B., Pankrath, J. (eds) (1983): Effects of Accumulation of Air Pollutants in Forest Ecosystems. Reidel Publ. Comp., Hingham.
- Woodman, J.N., Cowling, E.B. (1987): Airborne chemicals and forest health. Environm. Sc. and Technol., 21: 120-126.
- Zöttl, H.W., Mies, E. (1983): Nährelementversorgung und Schadstoffbelastung von Fichtenökosystemen im Südschwarzwald unter Immissionseinfluss. Mitt. Dtsch. Bodenk. Ges., 38: 429-434.
- Zöttl, H.W., Hüttl, R.F. (1985): Schadsymptome und Ernährungszustand von Fichtenbeständen im südwestdeutschen Alpenvorland. Allg. Forst. Zschr., 9/10: 197-199.

LOKALE INDUSTRIELLE EMISSION UND WALDSCHÄDEN IN NORDUNGARN III.
GESALTUNG DES NEBENWURZELWERKES UND DER MYKORRHIZA-BEZIEHUNGEN BEI
GESUNDEN UND KRANKEN BAUMEN

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The paper presents some parameters of the roots of Quercus petraea s. l. trees and the quantitative changes and the activity of the connected mycorrhiza in heavily air-polluted industrial areas and in control plots in North-Hungary. It verifies that the mycorrhiza connections have strongly degraded under the effect of air-polluting materials acting through the soil on the sampling sites near the industrial centre. In a longer distance from the emission sources the symbiotic root connections of the trees have remained more healthy. Studying the qualitative and quantitative features of mycorrhiza connections of healthy and diseased trees in the same site, significant differences could be observed. The paper demonstrates that there is a strong reduction in the number of mycorrhiza even in the roots of trees estimated as "healthy" ones. All these results seem to verify that the effect of the local pollution intensifies the weakening of the symbiotic tree-fungi relations caused also by the global air pollution and, after all, it amplifies the process of tree decline.

EINFÜHRUNG

Mit den Wurzeln zahlreicher Pflanzen leben gewisse Pilze in Symbiose. Diese Erscheinung wurde Mitte des vorigen Jahrhunderts von FRANK (1885) Mykorrhiza genannt. Der Begriff der Mykorrhiza wurde seitdem wesentlich erweitert. So werden heutzutage sämtliche symbiotische Beziehungen zwischen unterirdischen Pflanzenteilen und Pilzen bezeichnet, bei welchen die Pilze der Gastpflanze gegenüber keine Pathogenität zeigen (SZABÓ 1986).

Die überwiegende Mehrheit der waldbildenden Bäume des gemäßigten Klimas bilden mit den symbiotischen Pilzen Ektomykorrhiza, es kann jedoch auch Endomykorrhiza vorkommen. Die meisten Symbionten sind Basidiomyceten,

eine Ektomykorrhiza mit Askomyzeten kommt nur selten vor (AGERER et al. 1986, MARKS und KOZLOWSKI 1973).

Mit der Quercus Gattung Arten leben meistens die folgenden Gattungen als Pilzpartner in Symbiose: Amanita, Boletus, Gyroporus, Xerocomus, Lec-cinum, Lactarius, Russula, Cortinarius, Hebeloma, Inocybe, Tricholoma, Can-tharellus, Cratarellus, Helvella, Lepista, Lycoperdon und Pisolithus (TRAPPE 1962).

Eine symbiotische Verbindung ist für beide Partner vorteilhaft. In Anbetracht des Gastorganismus können folgende Vorteile erwähnt werden:

- besserer Wirkungsgrad der Wasser- und Nährelementenversorgung auch unter ungünstigen Bodenverhältnissen (z.B. in Perioden mit niedriger Bodenfeuchtigkeit)
- selektive Aufnahme gewisser Ionen aus dem Boden
- Übergabe einiger Hormone und Enzyme der Partnerpflanze
- grössere Toleranz gegenüber dem sich periodisch ändernden pH-Wert und den Anionen- bzw. Kationenkonzentrationen des Bodens
- optimales Wachstum und grössere Vitalität der Wurzeln
- erhöhte Toleranz gegenüber den Bodentoxinen
- Zunahme der Resistenz gegenüber den wurzelpathogenen Organismen (WINGFIELD 1968, MARX 1969, RICHARD et al. 1971, ROSS und MARX 1972, MARX 1972, MARKS und KOZLOWSKI 1973, HARLEY und SMITH 1983).

Bei den möglichen Ursachen des neuartigen Absterbens der Quercus petraea s.l. Bäume in Ungarn wird von den Ökologen — aufgrund zahlreicher Beweise — die Umweltverschmutzung, genauer gesagt die Luftverschmutzung auf den ersten Platz gesetzt. Durch die Luftschadstoffe werden die Bäume direkt geschädigt (vor allem die Nadelbäume), zahlreiche Tatsachen weisen jedoch darauf hin, dass ihre grösste Schadwirkung durch den Boden — durch Akkumulation — auf einem indirekten Weg entwickelt wird (JAKUCS 1983, JAKUCS et al. 1986).

Im geschädigten Waldbestand wurde auch in anderen Ländern Europas oft eine Reduktion der Mykorrhiza-Pilzflora und der Haarwurzel-dichte beobachtet (BLASCHKE 1981, VOGELMANN 1982, UHLRICH 1983, HÜTERMANN 1983, JAKUCS 1983, PAPP und PAPP 1983, GULDEN und HOILAND 1985, SCHLECHTE 1986, JAKUCS et al. 1986, MEYER 1987).

Das Absterben der Traubeneichen und der Degradationszustand der Wälder sind in Nordungarn im Wirkungsbereich des luftverschmutzenden Industriegebietes Sajó-Tal um eine Grössenordnung fortgeschrittener, als in anderen Gebieten des Landes. Nach unseren Annahmen sollten das Absterben

der besonders geschädigten Wälder und die durch den Boden entwickelte Schadwirkung der emittierten Luftschadstoffe der nahe liegenden Industriebetriebe, welche auch die Bodenqualität verändern, in enger Korrelation stehen. In unseren komplexen Forschungen wurden Qualität und Quantität der Mykorrhiza-Beziehungen und Nebenwurzeleigenheiten der Quercus petraea Bäume sowohl bei den geschädigten Waldbestände der industrienahen Gebiete, als auch bei den Kontrollbeständen entfernter liegender Gebiete untersucht (siehe noch JAKUCS und BABOS 1988, BERKI und HOLES 1988, JAKUCS et al. 1988).

UNTERSUCHUNGSMATERIAL UND METHODE

Im Sommer 1987 wurden in acht den industriellen Emissionsquellen näher liegenden (0,5–20 km) Probeentnahmestellen von dem Wurzelwerk inklusive Erdballen der Quercus petraea Bäume Proben entnommen. In den Probeentnahmestellen wurden jeweils gesunde und kranke Baumpaare untersucht. Als Kontrolle wurden in drei, vom Industriegebiet entfernter liegenden (18–35 km) Traubeneichenwäldern Proben entnommen. Die detaillierten Angaben der Probeentnahmestellen sind in der Veröffentlichung von JAKUCS et al. (1988) enthalten.

Vom Wurzelwerk der gekennzeichneten Bäume wurden jeweils 4 Proben vom Baumstamm entfernend in einer Tiefe von 10 bis 30 cm entnommen. Die optimale Tiefe der Probeentnahme wurde durch orientierende Prüfungen festgestellt. Die wurzelhaltigen Bodenproben wurden auf dem Weg zum Laboratorium gekühlt gehalten.

Bei der Verarbeitung der Proben im Laboratorium wurden diese für kurze Zeit ins Wasser gelegt. Anschliessend wurden die Wurzeln mittels Wasserstrahl vorsichtig, ohne die dünnen Wurzelzweige und die Mykorrhizen zu verletzen, ausgewaschen. Das so vorbereitete Probenmaterial wurde gleich verarbeitet.

Zur Charakterisierung des Nebenwurzelwerkes der gesunden und kranken Bäume verwendeten wir in unseren Untersuchungen folgende morphologische Parameter: Anzahl der Wurzelspitzen, Anzahl der aktiver und inaktiver Mykorrhiza, Anzahl der Wurzelspitzen ohne Mykorrhiza, gesamte Anzahl der Wurzelspitzen mit Mykorrhiza.

Für die Untersuchungen wurden aus den vorbereiteten Proben wahllos Wurzeln mit 1 mm Durchmesser je 20 Stück pro Baum entnommen. Aus den ausgewählten Wurzeln wurden 5 cm lange Segmente geschnitten. Unter Präpariermikroskop wurden auf diesen 5 cm langen Segmenten die Wurzelspitzen, die aktiven und inaktiven Mykorrhizen abgezählt. Die diesbezüglichen Hinweise der Fachliteratur wurden bei dieser Arbeit berücksichtigt (HARVEY et al. 1976, EGLI 1980, PAPP und PAPP 1983, SZEGI 1979, SZABÓ 1986). Die erhaltenen Ergebnisse wurden auf 5 cm bezogen.

Durch die statistische Verarbeitung der Daten wurden Mittelwert sowie Fehler und signifikante Differenz der Mittelwerte ermittelt.

Tabelle 1

Charakterisierung des Nebenwurzelwerkes bei gesunden (G) und kranken (K) Bäumen aufgrund der Mykorrhiza-Untersuchungen, entsprechend den Probeentnahmestellen (Die Durchschnittswerte sind in Stück/5 cm Wurzelsegment angegeben)

		Wurzelspitzen gesamt	Wurzelspitzen ohne Mykorrhiza	Inaktive Mykorrhiza	Aktive Mykorrhiza	Wurzelspitzen mit Mykorrhiza gesamt
Berente	G:	136.2 [±] 39.05	86.0 [±] 28.24	26.6 [±] 5.03	23.6 [±] 10.45	50.2 [±] 11.51
	K:	133.8 [±] 18.91	104.2 [±] 13.07	26.0 [±] 5.24	3.6 [±] 3.58	29.6 [±] 6.50
Sajóbábony	G:	131.0 [±] 24.87	81.8 [±] 20.33	30.8 [±] 7.29	18.4 [±] 2.61	49.2 [±] 7.85
	K:	130.0 [±] 29.07	65.0 [±] 36.69	45.6 [±] 15.50	18.0 [±] 19.80	63.6 [±] 33.11
Radostyán	G:	116.6 [±] 26.58	48.3 [±] 29.65	46.8 [±] 27.67	21.6 [±] 13.72	68.4 [±] 34.30
	K:	127.4 [±] 13.35	76.6 [±] 15.75	25.0 [±] 5.34	25.8 [±] 7.69	50.8 [±] 8.93
Tapolca	G:	155.2 [±] 21.12	53.0 [±] 4.69	82.0 [±] 27.49	20.2 [±] 5.12	102.2 [±] 24.18
	K:	149.6 [±] 30.15	100.8 [±] 23.32	37.0 [±] 12.04	11.8 [±] 4.32	48.8 [±] 15.09
Sajóivánka	G:	100.8 [±] 14.94	64.2 [±] 9.26	22.8 [±] 3.70	13.8 [±] 4.82	36.6 [±] 6.66
	K:	92.4 [±] 9.63	70.6 [±] 11.15	20.4 [±] 8.26	1.4 [±] 2.19	21.8 [±] 9.39
Kazinc- barcika	G:	149.4 [±] 34.15	34.8 [±] 23.87	34.4 [±] 13.50	80.2 [±] 7.98	114.6 [±] 14.24
	K:	109.2 [±] 12.28	61.2 [±] 5.50	28.6 [±] 8.44	19.4 [±] 6.47	48.0 [±] 10.30
Putnok	G:	100.8 [±] 16.78	52.6 [±] 9.07	29.8 [±] 7.05	18.4 [±] 6.23	48.2 [±] 11.52
	K:	83.4 [±] 22.10	62.8 [±] 17.05	16.0 [±] 5.39	4.6 [±] 3.65	20.6 [±] 7.02
Dédes- tapolcsány	G:	111.4 [±] 20.84	52.6 [±] 13.94	32.0 [±] 7.68	26.8 [±] 7.09	58.8 [±] 13.16
	K:	128.6 [±] 21.89	96.8 [±] 15.58	27.2 [±] 7.40	4.6 [±] 5.08	31.8 [±] 7.02
Nagyvisnyó ^x	G:	110.0 [±] 12.35	28.8 [±] 12.87	50.4 [±] 6.19	31.8 [±] 12.11	82.2 [±] 14.21
	K:	127.4 [±] 13.22	49.2 [±] 13.33	51.0 [±] 7.78	27.2 [±] 15.94	78.2 [±] 21.53
Répáshuta ^x Aggtelek ^x	G:	146.2 [±] 18.39	70.0 [±] 13.11	37.8 [±] 4.66	38.4 [±] 6.27	76.2 [±] 9.24
	G:	145.7 [±] 52.50	14.8 [±] 10.86	34.8 [±] 14.39	96.0 [±] 35.98	130.8 [±] 51.57

Kontrollgebiete mit (x) gekennzeichnet

ERGEBNISSE

Die Ergebnisse der Untersuchungen wurden je Probeentnahmestelle in Tabelle 1 zusammengefasst.

Zur Charakterisierung der Mykorrhiza-Beziehungen von kranken und gesunden Bäumen können folgende Feststellungen genannt werden, wobei der Durchschnitt der Mykorrhiza-Merkmale von gesunden und kranken Bäumen separat gebildet wird: Zwischen den gesunden und sterbenden Bäumen gibt es Unterschiede in der durchschnittlichen Anzahl der Wurzelspitzen bezogen auf 5 cm lange Wurzelsegmente, in der durchschnittlichen Menge der Wurzelspitzen mit aktiven und inaktiven Mykorrhiza, in der durchschnittlichen Menge der Wurzelspitzen ohne Mykorrhiza und in der gesamten Menge der Wurzelspitzen mit Mykorrhiza (Tabelle 2).

Tabelle 2

Nebenwurzel- und Mykorrhiza-Merkmale der gesunden und kranken Bäume (die Durchschnittswerte sind in Stück/5 cm Wurzelsegment angegeben)

Untersuchungsparameter	gesunde Bäume (n=220)	kranke Bäume (n=180)
Wurzelspitzen gesamt	127.55 [±] 20.21	120.05 [±] 21.12
Wurzelspitzen ohne Mykorrhiza	53.35 [±] 21.75 ^(xx)	76.36 [±] 19.70
Inaktive Mykorrhiza	38.93 [±] 16.42	30.76 [±] 11.55
Aktive Mykorrhiza	25.28 [±] 27.19 ^(x)	12.93 [±] 9.98
Wurzelspitzen mit Mykorrhiza gesamt	74.31 [±] 30.41	43.69 [±] 19.48

Signifikanzstufen: (xx) = 1%

(x) = 5%

Nicht signifikant, dennoch unterschiedlich sind die durchschnittlichen Mengen der Wurzelspitzen auf den 5 cm langen Wurzelsegmenten bei gesunden und kranken Bäumen (gesunde Bäume: 127.55 Stück; kranke Bäume: 120.05 Stück). Unter den kranken Bäumen sind signifikant mehr Wurzelspitzen ohne Mykorrhiza zu finden (gesunde Bäume: 53.35 Stück; kranke Bäume: 76.36 Stück).

In der Anzahl der inaktiver Mykorrhiza zeigte sich eine nicht signifikante Differenz für die gesunden Bäume. Signifikant ist demgegen-

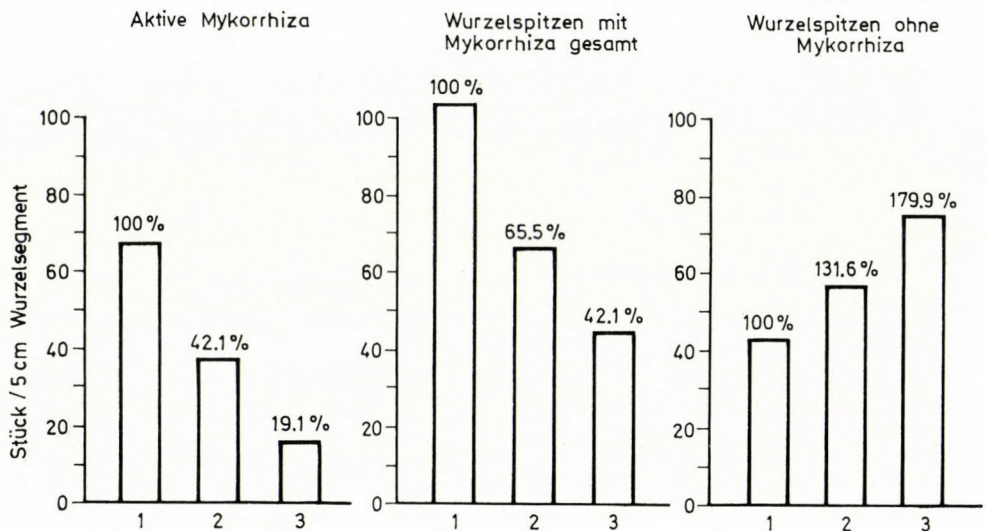


Abb. 1. Verhältnis Wurzelspitze/Mykorrhiza in den durch die Luftverschmutzung des Industriegebietes Sajó-Tal geschädigten Gebieten, angegeben in Prozent der Kontrollwerte. 1 = gesunder Wald, gesunde Bäume (n:12), entfernt von der Industrie, Kontrolle. 2 = kranker Wald, gesunde Bäume (n:45), nahe zur Industrie. 3 = kranker Wald, kranke Bäume (n:45), nahe zur Industrie

über den Unterschied zwischen den kranken und gesunden Bäumen hinsichtlich der Anzahl der aktiven Mykorrhiza (G: 25.28 Stck.; K: 12.93 Stck.) sowie der gesamten Anzahl der Wurzelspitzen mit Mykorrhiza (G: 74.31 Stck.; K: 43.69 Stck.).

Es ist beachtenswert, dass während bei den gesunden Bäumen die Wurzeln zu 19.81% aktive Mykorrhiza zeigen und der Anteil der Wurzelspitzen mit Mykorrhiza (aktive und inaktive zusammen) 50.34% beträgt, bei kranken Bäumen diese Werte nur 10.77% erreichen. Zwischen dem Gesundheitszustand der Bäume und ihren quantitativen Mykorrhiza-Beziehungen besteht also eine enge Korrelation.

Die Untersuchungsparameter der industrienahen und entfernteren liegen den Mustergebiete wurden ebenfalls verglichen. Mit der Berücksichtigung der geographischen Lage der Probeentnahmegebiete, ihrer Entfernung von den Industriezentren sowie der erhaltenen Mykorrhizaparameter, kann eindeutig festgestellt werden, dass die Menge der aktiven und inaktiven Mykorrhizen auf dem Wurzelwerk der untersuchten Bäume und die gesamte Menge der Wurzelspitzen mit Mykorrhiza eine starke Abhängigkeit von der Entfernung der luftverschmutzenden Quellen zeigen (Abb. 1). Die Mykorrhiza-Beziehungen in den industrienahen Gebieten sind im Vergleich zu denen in den Kontrollgebieten

schwer degradiert. Das Verhältnis aktive Mykorrhiza/gesamte Mykorrhiza erreicht in diesen Gebieten (Berente, Dédestapolcsány, Sajóivánka, Putnok, Sajóbáony, Rodostyán) im Vergleich mit den Kontrollgebieten einen Minimalwert bei den kranken Bäumen und sogar bei den gesunden Bäumen ist dieser Wert sehr niedrig. Entfernt man sich von den industriellen Luftschadstoffquellen, so findet man in den Gebieten, wo die atmosphärische Immission – unter Berücksichtigung der meteorologischen und orographischen Verhältnisse – niedriger ist, ebenfalls störungsfreie symbiotische Beziehungen. In der Abbildung 1. werden auch die Mittelwerte der wichtigsten gemessenen Parameter bezogen auf die Kontrollgebiete in Prozent angegeben.

DISKUSSION

Werden unsere Untersuchungsdaten dahingehend überprüft, ob ein Zusammenhang zwischen den vorgestellten Mykorrhiza-Merkmalen und den bodenchemischen Parametern unter denselben Bäumen, dem Mineralstoffgehalt der Blätter sowie der Verstopfung der wasserleitenden Gefäße des Stammes besteht, so können folgende Feststellungen formuliert werden (BERKI und HOLES 1988, JAKUCS und BABOS 1988).

Durch die, von den Luftschadstoffen hervorgerufene, Verminderung des pH-Wertes im Boden werden die Mykorrhiza-Beziehungen negativ beeinflusst (KARAGIANNIDIS et al. 1981, SCHAFER 1985, JAKUCS et al. 1986). Es ist bekannt, dass der pH-Wert des Bodens bestimmt, ob die Mykorrhiza-Pilze fähig sind den Phosphorgehalt des Bodens für die Gastpflanze mobilisieren zu können. Durch den pH-Wert wird ebenfalls die Effizienz der Gestaltung der Mykorrhiza-Beziehungen beeinflusst (MEYER 1962, AGERER et al. 1986, SZABÓ 1986). Die Versauerung des Bodens bringt die Mobilisation einiger Schwermetalle und des Aluminiums im Boden mit sich. Diese Prozesse hemmen die Bildung der Mykorrhiza, schädigen das Wurzelmeristem, vermindern die Permeabilität der Wurzelzellen, verhindern die Wasseraufnahme und rufen Störungen in der Wurzelentwicklung hervor (BLACK 1968, FOY 1982, ULRICH et al. 1979, 1983, JAKUCS 1983). In solchen, sich rasch versauernden Böden wird die Mykorrhiza-Symbiose geschädigt und zurückgedrängt, die Übergabe der für die Gastpflanze wichtigen Auxine, Phytohormone und gewisse Kohlenhydrate entfällt (SLANKIS 1971, VELDEMAN 1980, DAVID et al. 1983, MEYER 1985). Die Schutzfunktion der Pilzhülle gegenüber den pathogenen Organismen und toxischen Ionen wird aufgehoben.

Bei Annäherung an die Emissionsquellen in den untersuchten Gebieten nahm die Konzentration des Nitrat-Stickstoffes im Boden zu (BERKI und HOLES 1988). Durch den Nitrat-Stickstoff-Überschuss selbst — welcher in diesem Fall ausschliesslich nur von der industriellen Luftverschmutzung stammen kann — wird die Effizienz der symbiotischen Beziehungen im Boden, die Entwicklung und die Anzahl der Mykorrhizen drastisch reduziert (MENGE et al. 1977a,b, OHENOJA 1978, ALEXANDER und FAIRLY 1983, BLAISE und GARBAYE 1983, MEYER 1985, ZEJSCHWITZ 1985).

In den Chemiebetrieben des untersuchten Gebietes werden auch Pflanzenschutzmittel und dabei auch Fungizide hergestellt, letztere können ebenfalls unter den Luftschadstoffen aufgefunden werden. Diese Verbindungen verfügen über eine bewiesenen mykorrhizahemmende Wirkung (WINGFIELD 1968, DEHNE und SCHÖNBECK 1981, LAKE et al. 1981).

Die Degradierung des Wurzelwerkes und der symbiotischen Pilzbeziehungen der Bäume kann letzten Endes die Störung des Wasser- und Nährstoffkreislaufes und den Stresszustand des Baumes hervorrufen (JAKUCS 1983, JAKUCS et al. 1986). Die Verstopfung der wasserleitenden Gefässe der Bäume (JAKUCS und BABOS 1988) und die Störung der Nährstoffaufnahme können in der chemischen Zusammensetzung der Laubblätter indiziert werden (BERKI und HOLES 1988).

Die vorgestellten Daten beweisen, dass mit zunehmender Entfernung von den industriellen Emissionsquellen die Mykorrhiza-Beziehungen der Bäume "gesünder" werden. In den industrienahen Wäldern findet man sogar bei den "gesund" erklärten Bäumen eine starke Reduktion in der Anzahl der Mykorrhizen und die Zurückdrängung der Symbiose. Dies scheint zu bestätigen, dass die — durch globale Luftverschmutzung hervorgerufene — Abschwächung der Pilz-Baum-Beziehungen und letzten Endes der Absterbevorgang der Bäume durch die Wirkung der lokalen Luftverschmutzungsquellen verstärkt werden.

LITERATUR

- Agerer, R., Brand, F., Gronbach, E. (1986): Die exakte Kenntnis der Ectomycorrhizen als Voraussetzung für Feinwurzeluntersuchungen im Zusammenhang mit dem Waldsterben. Allg. Forst Zschr., 20: 497–503.
- Alexander, I.J., Fairly, R.I. (1983): Effects of N fertilization on populations of fine roots and mycorrhizas in spruce humus. Plant and Soil, 71: 49–53.
- Berki, I., Holes, L. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn II. Mineralstoffgehalt des Bodens und der Blätter von Quercus petraea s.l. Acta Bot. Hung., 34: 25–37.

- Black C.A. (1968): Soil-Plant Relationships. 2nd ed., Wiley, New York.
- Blaise, T. Garbaye, I. (1983): Effect of mineral fertilization on the mycorrhization of rocts in beech forest. Oecol. Plant., 4: 165-170.
- Blaschke, H. (1981): Veränderungen die der Feinwurzelentwicklung in Weisstannenbeständen. Forstwiss. Cbl., 100: 190-195.
- David, A. Faye, M., Rancillac, M. (1983): Influence of auxin and micorrhizal fungi on the in vitro formation and growth of Pinus pinaster roots. Plant and Soil, 71: 501-505.
- Denhe, H.W., Schönbeck, F. (1981): Influence of systemic chemicals on the development of VA-mycorrhiza. North Am. Conf. on Mycorrhizae, Quebec, Canada, Abstracts 50.
- Egli, S. (1980): Vertikale Verteilung der Mycorrhiza in Eichenbeständen Zusammenhang mit der Bewurzelung und einzelnen edaphischen Merkmalen. Diplomarbeit. (Mskr.).
- Foy, C.D., Fleming, A.L. (1982): Aluminium tolerances of two wheat genotypes related to nitrate reductase activities. J. Plant. Nutr., 5: 1313-1333.
- Frank, A.B. (1885): Über die auf Wurzelsymbiose beruhende Ernährung gewisser Bäume durch unterirdische Pilze — Ber. d. Deutsch. Bot. Ges., 3: 128-145.
- Gulden, G., Hoiland, K. (1985): The role of ectomycorrhiza in a situation of air pollution and forest death. Agarica, 6: 341-357.
- Harley, J.L., Smith, S.e. (1983): Mycorrhizal Symbiosis, Academic Press, London-New York.
- Harvey, A.E., Larsen, M.J., Jurgensen, M.F. (1976): Distribution of ectomycorrhizae in a mature douglas-fir/larch forest soil in western Montana. Forest Sci. 22: 393-398.
- Hüttermann, A. (1983): Frühdiagnose von Immissionsschäden im Wurzelbereich von Waldbäumen. In: Immissionsbelastungen in Waldökosystemene, LÖLF Nordrhein-Westfalen, 26-31.
- Jakucs, P. ed. (1983): Ökologische Untersuchung des Gesundheitszustandes von Eichenbeständen in Ungarn. (Mskr.).
- Jakucs, P. (1985): Summarizing the trends of element-movement in the forest. In: Jakucs (ed.): Ecology of an Oak Forest in Hungary, Results of Sífőkút Project 1. Akadémiai Kiadó, Budapest, 511-526.
- Jakucs, P., Mészáros, I., Papp, B.L., Tóth, J.A. (1986): Acidification of soil and decay of sessile Oak in the "Sífőkút Project" area (N-Hungary). Acta Bot.Hung., 32: 303-322.
- Jakucs, P., Babos, K. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn IV. Jahringbreiten und Tracheenverstopfungen von gesunden und erkrankten Quercus petraea Stämmen. Acta Bot. Hung., 34: 51-64.
- Jakucs, P., Berki, I., Holes, L., Tóthmérész, B. (1988): Lokale industrielle Emission und Waldschäden in NordUngarn I. Problemstellung, Ausgangshypothese und Zusammenfassende Wertung. Acta Bot. Hung., 34: 11-24.
- Karagiannidis, Nikitas, Khanaga, Azad and Moawad (1981): Influence of soil pH on the efficiency of VA-mycorrhiza. North Am. Conf. on Mycorrhizae, Quebec, Canada, Abstracts 18.

- Lake, D.B., Ippoliti, D.J., Brandow, C.C. (1981): Effect of herbicides on the growth of Pisolithus tinctorius and Scleroderma aurantium in pure culture. North Am. Conf. on Mycorrhizae, Quebec, Canada, Abstracts 62.
- Marks, G.C., Kozlowski, T.T. (1973): Ectomycorrhizae: Their Ecology and Physiology. Academic Press, New York-London.
- Marx, H.D. (1969): The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology 59: 153-163.
- Marx, H.D. (1972): Ectomycorrhizae as biological deterrents to pathogenic root infections. Ann. Rev. Phytopathology, 10: 429-454.
- Menge, J.A., Grand, L.F. (1977a): Effect of fertilization on production of epigeous basidiocarps by mycorrhizal fungi in loblolly pine plantations. Can. J. Bot., 56: 2357-2362.
- Menge, J.A., Grand, L.F., Haines, L.W. (1977b): The effect of fertilization on growth and mycorrhizae numbers in 11-year old loblolly pine plantations. For. Sci., 23: 37-44.
- Meyer, F.H. (1962): Die Buchen und Fichtenmykorrhiza in verschiedenen Böden, ihre Beeinflussung durch Mineraldünger sowie für die Mykorrhizabildung wichtige Faktoren. Mitt. Bundesforsch. Anst. Forst-Holzwirtsch., 54: 1-73.
- Meyer, F.H. (1985): Einfluss des Stickstoff-Factors auf den Mykorrhizabesatz von Fichtensämlingen im Humus einer Waldschadensfläche. Allg. Forst. Zschr., 40: 97-99.
- Meyer, F.H. (1987). Das Wurzelsystem geschädigter Waldbestände. Allg. Forst Zschr., 27/28/29: 754-757.
- Ohenoja, E. (1978): Mushrooms and mushroom yields in fertilized forests. Ann. Bot. Fennici, 15: 38-46.
- Papp, B.L., Papp, M. (1984). Comparative investigations on the roots of healthy and dying sessile oak seedlings.(in Hung.) Az Erdő, 33: 345-347.
- Richard, C., Fortin, I.A., Fortin, A. (1971): Protective effect of an ectomycorrhizal fungus against the root pathogen Mycelium radicis atrovirens. Can. J. For. Res., 1: 246-251.
- Ross, E.W., Marx, H.D. (1972): Susceptibility of stand pine to Phytophthora cinnamomi. Phytopathology, 62: 1197-1200.
- Schafer, M. (1985): Waldschäden und die Tierwelt des Bödens. Allg. Forst Zschr., 27: 676-679.
- Schlechte, G. (1986): Zur Mykorrhizapilzflora in geschädigten Forstbeständen. Zschr. f. Mykologie, 52: 225-232.
- Slankis, V. (1971): Formation of ectomycorrhizae of forest trees in relation to light, carbohydrates and auxins. In: Hacskeylo (ed.): Mycorrhizae. U. S. Dept. Agric. Misc. Publ., 1189: 151-167.
- Szabó, I.M. (1986): Biologische Grundlagen der allgemeinen Bodenkunde (ungarisch). Mezőgazdasági Kiadó, Budapest.
- Szegi, J. (1979): Untersuchungsmethoden der Bodenmikrobiologie (ungarisch). Mezőgazdasági Kiadó, Budapest.

- Trappe, I.M. (1962): Fungus associates of ectotrophic mycorrhizae. Bot. Rev., 28: 538-606.
- Ulrich, B. (1983): Gefahren für das Waldökosystem durch saure Niederschläge. In: Immissionsbelastungen von Waldökosystemen, LÖLF Nordrhein-Westfalen, 9-25.
- Ulrich, B., Mayer, R., Khanna, P.K. (1979): Deposition von Luftverunreinigungen und ihre Auswirkungen in Waldökosystemen im Solling. Schriften Forstl. Fak. Univ. Göttingen, 58: 1-291.
- Veldeman, I.R. (1980): Influence of mycorrhizae on the rooting of poplar (*Populus nigra italica*). Med. Fac. Landbouwet. Riksuniv. Gent, 45: 169-174.
- Vogelman, H.W. (1982): Catastrophe on Camels Hump. Natural History, 11: 8-14.
- Wingfield, E.B. (1968): Mycotrophy in loblolly pine. I. The role of Pisolithus tinctorius and Rhizoctonia solani in survival of seedlings. II. Mycorrhiza formation after fungicide treatment. Ph. D. Thesis. Virginia Polytech. Inst., Blacksburg.
- Zeischwitz, E. (1985): Qualitätsänderungen des Waldhumus. Forstw. Cbl., 104: 205-220.

LOKALE INDUSTRIELLE EMISSION UND WALDSCHÄDEN IN NORDUNGARN IV.
JAHRRINGBREITEN UND TRACHEENVERSTOPFUNGEN VON GESUNDEN UND
ERKRANKTEN QUERCUS PETRAEA (MATT.) LIEBL. STAMMEN

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The air-pollution caused by the chemical industry, metallurgical and machine industry and by the coal-heated power stations in North-Hungary surpasses the national average. In the area surroundings of the factories within an area of 1 to 12 kms the "new-type forest decay" is stronger than in the farther control areas. The annual rings in the trunks and the degree of the obstruction by tyloses in the water and nutrient carrying vascular tissues were investigated in both healthy and diseased sessile oak individuals. It was stated that the tree decay is larger and quicker near the air polluting industrial establishments and a remarkable production loss of the healthy individuals may also take place.

In Zusammenhang mit dem neuartigen Baumsterben wurde in Ungarn über die Untersuchung von Jahrringbreiten und Tracheenverstopfungen der Traubeneichen (Quercus petraea (Mattuschka) Liebl.) wenig veröffentlicht (JAKUCS und TÓTH 1984, JAKUCS et al. 1986, IGMÁNDY et al. 1986, BABOS et al. 1985, BABOS 1987). Durch die Analyse dieser zwei histologischer Parameter werden jedoch recht viele Teilinformationen über den Ablauf der Erkrankung sowie über die organische Stoffspeicherung (Holzproduktion) während dieser Zeit gewonnen. Die vorliegende Veröffentlichung bildet einen Teil eines komplexen Forschungsprogrammes, in welchem Wälder nahe industrieller Emission sowie davon entfernt liegender (Kontroll) gebiete geprüft werden. Die Untersuchungen erstrecken sich auch auf die Bodenverhältnisse der gesunden und erkrankten Bäume, auf die chemische Zusammensetzung der Blätter sowie auf Gestaltung der symbiotischen Verbindungen des Wurzelwerkes (JAKUCS et al. 1988, BERKI und HOLES 1988, HOLES und BERKI 1988).

UNTERSUCHUNGSMETHODE

Die gekennzeichneten Bäume wurden gefällt und in einer Höhe von 1.3 m vom Boden gemessen wurden aus dem Stamm Scheiben geschnitten, deren Oberflächen glatt gehobelt wurden.

Die Jahrringanalysen wurden mit dem Ernst-Leitz-Wetzlar-Mikroskop bei einer 30-fachen Vergrößerung durchgeführt, zurückgehend auf die vergangenen 20 Jahre. Die Messungen wurden bei jeder Scheibe in vier Richtungen durchgeführt (in der längsten Strecke zwischen Mark und Rinde, in der kürzesten Strecke zwischen Mark und Rinde, sowie senkrecht auf diese Strecken). Die Jahrringbreiten wurden also immer aus 4 parallelen Daten errechnet. Die Jahrringbreite ergibt sich bei den Eichen aus der Zuwachssumme von Früh- und Spätholz.

Auf den Scheiben von der Rinde her betrachtet enthält der noch nicht verkernte Splintteil in der Regel 8 bis 15 Jahrringe. Am Rand der gesamten Scheibe wurden die darauf senkrechten Markstrahlen sowie die zwischen ihnen liegenden offenen bzw. verstopften Tracheen abgezählt. Der Verstopfungsgrad (in %) einzelner Ringabschnitte des Splints wurde auch graphisch dargestellt (Abb. 1.). Das Mass der durchschnittlichen Tracheenverstopfung der Bäume wurde aufgrund dieser Daten festgestellt. Diese Arbeit wurde mit einem Binokular-Stereomikroskop (Zeiss) bei einer 16-fachen Vergrößerung durchgeführt.

Die detaillierten Angaben der Probeentnahmestellen sind in der Veröffentlichung von JAKUCS et al. (1988) erhalten.

UNTERSUCHUNGSERGEBNISSE

Jahrringbreite

Die gemessenen Daten wurden in Grundtabellen geordnet. Sowohl bei den "erkrankten" und "gesunden" Bäumen des Industriegebietes, als auch bei den gesunden Bäumen des Kontrollgebietes wurden die Mittelwerte für die jährlich gemessenen Jahrringbreiten ermittelt, einerseits in den letzten 10 Jahren vor dem Fällen bzw. in den vorhergehenden 10 Jahren, andererseits in den gesamten letzten 20 Jahren (Tabellen 1-3). Die Veränderung der jährlichen Mittelwerte der drei Variationen in Abhängigkeit von der Zeit wurde auch graphisch dargestellt (Abb. 2.).

Auf dem Untersuchungsgebiet befinden sich drei meteorologische Stationen (Putnok, Kazincbarcika und Miskolc), deren Jahresmittelwerte bezüglich des Niederschlages für die letzten 10 Jahre von uns errechnet wurden. Diese Daten wurden mit den gemessenen Jahrringbreiten der entsprechenden

Abb. 1. Prozentuale Verteilung der verstopften Tracheen im Splint (G = gesunde Bäume, K = kranke Bäume, A = Mittelwerte der Tracheenverstopfung, B = Tracheenverstopfung der einzelnen Segmente im Splint. 1-11 s. Tab. 4 und JAKUCS et al. 1988, Abb. 1.)

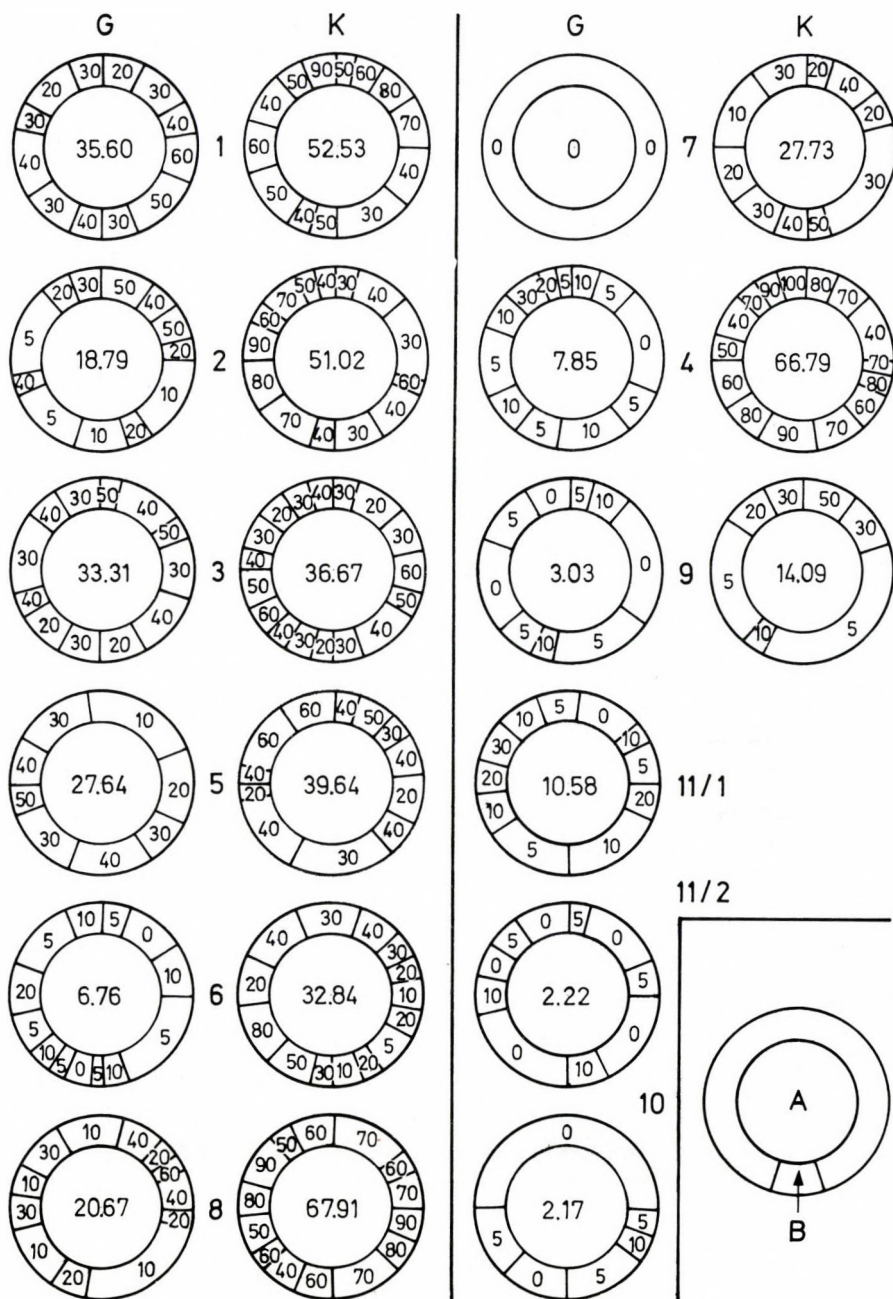


Tabelle 1

Jahrringbreiten der gesunden Bäume eines erkrankten Waldes im Industriegebiet Sajó-Tal (µm). 1-9 siehe Tab. 4.

		1	2	3	5	6	8	4	7	9	Durchschnitts- werte
	1986	1550	1075	1250	1150	850	725	900	775	1250	1058
	1985	1700	1175	1825	1225	1225	975	1075	475	1450	1236
	1984	3150	1000	2350	1775	1625	1250	1125	500	1525	1589
	1983	2275	1025	1550	1325	1200	1475	925	725	1325	1314
	1982	1950	875	1575	1150	1000	1150	950	700	1175	1169
	1981	1675	1250	1675	1350	1750	1700	1125	1100	1325	1439
	1980	2400	725	2150	1550	2250	2975	1225	1125	1100	1722
	1979	3350	975	1700	1425	1975	2975	1275	1250	1450	1819
	1978	2800	1050	700	425	775	2100	1000	800	875	1169
	1977	2700	1100	650	400	1275	2375	1075	800	1000	1264
	1976	1950	925	375	550	950	525	725	1125	1025	905
	1975	2275	750	550	675	675	575	1100	675	975	917
	1974	2375	775	500	925	1175	675	1475	1150	1500	1172
	1973	1775	1000	400	325	375	600	1100	425	975	775
	1972	2050	850	500	500	700	850	1075	425	1500	939
	1971	2525	900	375	775	1100	775	725	550	750	942
	1970	2025	900	350	1625	500	1025	900	875	775	997
	1969	2525	925	550	2375	1325	1200	950	875	850	1286
	1968	1975	825	675	1700	1200	1075	1350	800	725	1285
	1967	1975	925	550	1175	600	700	725	775	650	897
Durch-	(1967-86)	2300	951	1013	1120	1126	1285	1040	796	1110	1194
schnitts-	(1977-86)	2355	1015	1542	1177	1392	1770	1067	825	1247	1378
werte	(1967-76)	2245	877	482	1062	860	860	1012	767	972	1011

Tabelle 2

Jahrringbreiten der kranken Bäume eines erkrankten Waldes im Industriegebiet Sajó-Tal (μm). 1-9 siehe Tab. 4.

		1	2	3	5	6	8	4	7	9	Durchschnitts- werte
	1986	575	375	600	975	325	500	600	375	300	514
	1985	600	475	750	975	325	525	450	300	225	514
	1984	525	500	1150	950	350	700	600	475	300	617
	1983	750	625	850	925	500	700	400	625	325	633
	1982	875	675	975	1000	575	650	550	775	450	725
	1981	925	850	1275	1375	575	600	700	975	575	872
	1980	925	1125	1575	1400	600	750	700	1450	1275	1089
	1979	1200	900	1450	825	475	525	625	1575	1125	967
	1978	925	1175	1125	575	575	550	675	875	1250	858
	1977	850	1350	1000	550	550	600	650	1050	1075	853
	1976	1025	1100	625	1000	600	450	575	875	1275	836
	1975	1025	1025	775	1575	900	600	575	825	1500	978
	1974	900	1100	725	1425	775	575	675	1450	925	950
	1973	1225	1075	600	950	650	525	525	500	1575	847
	1972	1425	1125	600	1075	800	775	625	750	1150	925
	1971	1425	1000	625	1725	750	700	475	975	1100	975
	1970	1800	1125	725	1925	1300	850	625	825	925	1122
	1969	1725	1475	675	2325	1250	1125	675	1150	1200	1289
	1968	1975	1000	1000	2950	1125	1075	875	1150	1000	1350
	1967	1425	1175	925	2050	1225	800	575	975	1400	1172
Durch- schnitts- werte	(1967–86)	1105	962	901	1328	711	679	606	898	938	904
	(1977–86)	815	805	1075	955	485	610	595	847	690	764
	(1967–76)	1395	1120	727	1700	937	747	660	947	1205	1044

Tabelle 3

Jahrringbreiten der gesunden Bäume eines gesunden Waldes (Kontrollgebiet), (µm). 10-11 siehe Tab. 4.

		10	11/1	11/2	Durchschnitts- werte
	1986	1575	1500	1600	1558
	1985	1925	2075	1425	1808
	1984	2500	1800	1825	2042
	1983	2075	1800	1800	1892
	1982	2150	1325	1150	1542
	1981	1900	1650	1725	1758
	1980	1725	1950	1550	1742
	1979	1950	1950	1875	1925
	1978	1575	1500	1525	1533
	1977	2125	1700	1250	1692
	1976	1750	1675	1375	1600
	1975	1250	1150	875	1092
	1974	1850	1675	1250	1592
	1973	1475	925	700	1033
	1972	1500	1625	1325	1483
	1971	900	2225	1150	1425
	1970	1175	1775	1175	1375
	1969	2025	1950	1425	1800
	1968	1875	2100	1375	1783
	1967	1400	1375	1350	1375
Durchschnitts- werte	(1967-86)	1735	1686	1386	1602
	(1977-86)	1950	1725	1572	1749
	(1967-76)	1520	1648	1200	1456

Zeitpunkte in Korrelation gestellt (Abb. 3.). Auf den zur Industrie näher liegenden Gebieten ist der Korrelationskoeffizient (r) bei den gesunden Bäumen signifikant, der Zusammenhang ist stärker als der Durchschnitt. Bei den kranken Bäumen ist der r -Wert nicht signifikant und weist auf einen durchschnittlichen Zusammenhang hin. Die tiefere Lage der Regressionskurve bei den kranken Bäumen ist ein Zeichen dafür, dass diese Bäume in der photosynthetischen primär Produktion nur noch schwach auf die Niederschlagsmengen reagieren konnten, anders ausgedrückt: auch die reichlichen Niederschläge konnten den Zuwachs des Holzmaterials nicht mehr beeinflussen.

Aus der 2. Abbildung geht eindeutig hervor, dass die Jahrringbreiten der gesunden Bäume in den Kontrollgebieten in sämtlichen Fällen grösser sind, als die der gesunden Bäume in den Industriegebieten. Darauf weist auch jene Tatsache hin, dass in den zur Industrie näher liegenden Gebieten der Zuwachs der gesunden Bäume in den vergangenen 20 Jahren niedriger ist als in den Gebieten mit geringerer Luftverschmutzung. Sollten

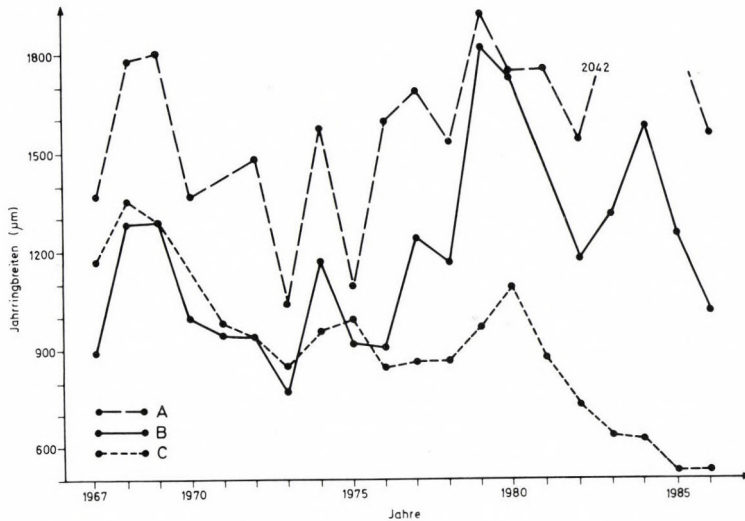


Abb. 2. Durchschnittswerte der Jahrringbreiten in den vergangenen 20 Jahren (A = Kontrollgebiet, gesunde Bäume, B = Industrie-Bezirk, gesunde Bäume, C = Industrie-Bezirk, kranke Bäume)

die durchschnittlichen Jahrringbreiten der Kontrollbäume in den letzten 10 Jahren als 100% bezeichnet werden, so liegt dieser Wert bei den "gesunden" Bäumen der stark verunreinigten Industriegebiete bei 68.7% und bei den erkrankten Bäumen bei 43.7%.

Zum Vergleich der zwei Durchschnittswerte bei den "gesunden" und "erkrankten" Bäume des Industriegebietes wurde die sog. t-Probe verwendet. Wenn m_1 und m_2 unabhängige Proben aus zwei normaler Verteilung mit gleicher Streuung bezeichnen, so kann mittels der t-Probe überprüft werden, ob die wirklichen Mittelwerte der zwei Grundmengen verschieden sind, oder die Abweichung der errechneten Mittelwerte nur ein Zufall ist. Wenn der errechnete absolute t-Wert kleiner oder gleich ist mit dem t-Wert der Tabelle, so kann $m_1 = m_2$ (Nullhypothese) mit der gegebenen α Sicherheit angenommen werden. Die $(100-\alpha)$ -Werte sind in der Abbildung 4. dargestellt. Dies bestätigt die Tatsache, dass seit 1977 die Wahrscheinlichkeit einer gleichen Zuwachsrates bei "erkrankten" und "gesunden" Bäumen fast 0% ist. Mit anderen Worten: es kann praktisch mit 100%-iger Sicherheit festgestellt werden, dass die Zuwachsrates bei "erkrankten" und "gesunden" Bäumen abweichen. 1976 und in den vorhergehenden Jahren besteht praktisch kein wesentlicher Unterschied zwischen den "gesunden" und "erkrankten" Bäumen bezüglich des Wachstums.

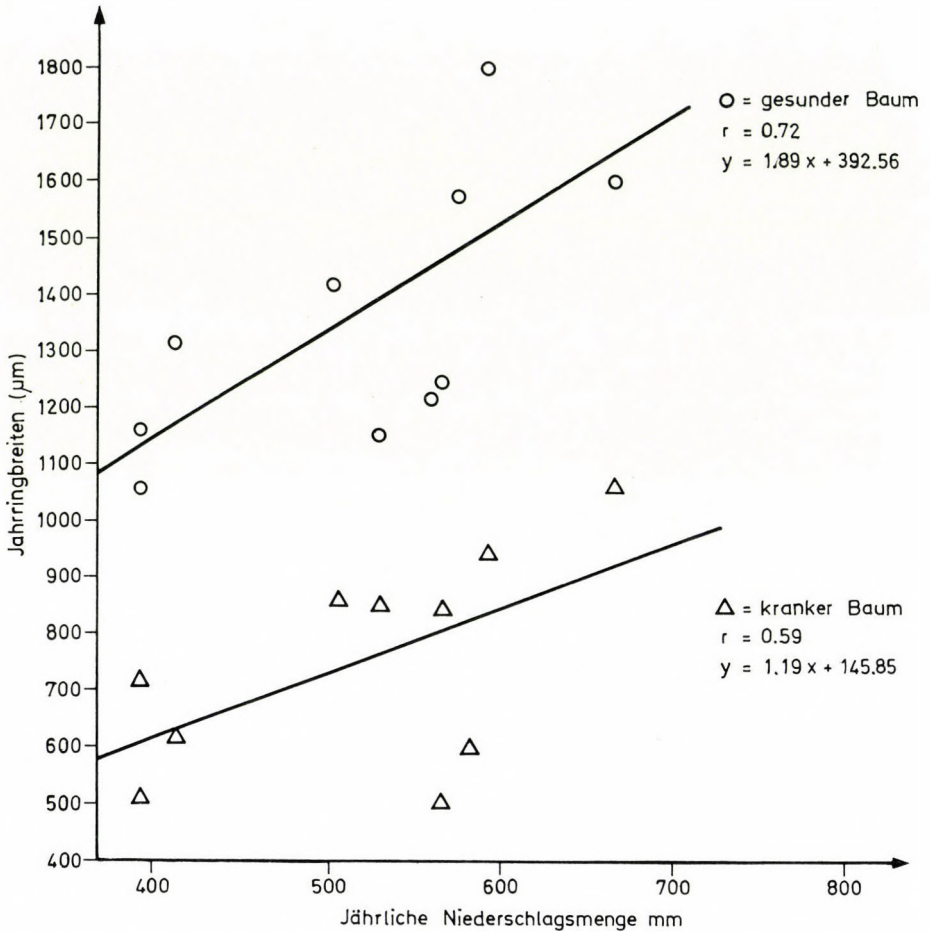


Abb. 3. Zusammenhang der Mittelwerte von Jahringbreiten und des jährlichen Niederschlags (1977–1986)

Dieser Vorgang wird in Abbildung 5. recht anschaulich gezeigt, wo die Veränderung der t-Werte für das Errechnen der Signifikanzniveaus dargestellt wird. Die t-Werte sind bis 1976 niedrig, ab 1977 nehmen sie jedoch stark zu. Dies weist auf eine bedeutende Baumschädigung ab 1977 hin, die Wachstumsgeschwindigkeit der "gesunden" und "kranken" Bäume wird signifikant unterschiedlich.

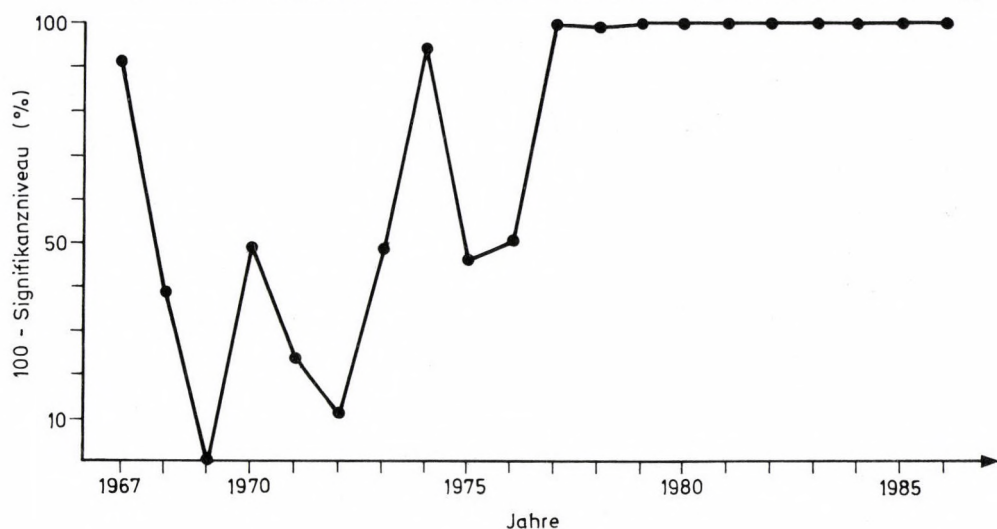


Abb. 4. Signifikanzwerte der Abweichung für den jährlichen durchschnittlichen Jahrringzuwachs bei gesunden und kranken Bäumen, in Prozenten angegeben

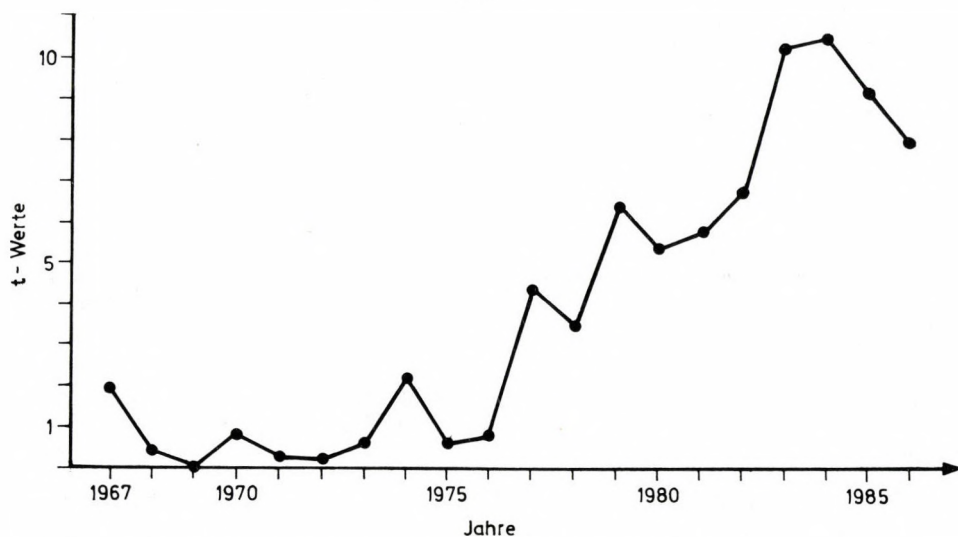


Abb. 5. Errechnete t-Werte beim Vergleich der jährlichen durchschnittlichen Jahrringzuwachsrate bei gesunden und kranken Bäumen

Tracheenverstopfung

In der Fachliteratur werden die in die wasser- und nährstofffördernden Gefäße der Bäume hineinwachsenden Zellen oder nicht zellartigen Blasen als Füllzellen bzw. Thyllen bezeichnet. Der Vorgang wird selbst Thyllenbildung genannt. Durch das Leitgewebe werden oft auch viskose Gele ausgeschieden. Sämtliche Erscheinungen, durch welche die Transportgänge verstopft werden, sind Schutzmechanismen des Baumes z.B. gegenüber ins Gefäß gelangter Luft oder toxischer Chemikalien, eventuell auch gegenüber einem Weiterkommen pathogener Mikroorganismen. Nach JACOBI und MCDONALD (1980) können in den pilzhaltigen Gefäßen der Quercus-Arten keine Füllzellen entstehen. SAVVIN (1981) bewies die Thyllenbildung auch in der Praxis durch Verletzen des Baumes sowie durch Belüften der Gänge. Die Tracheenverstopfung wird durch physiologisch verschiedene Enzyme und Hormone ausgelöst (BECKMANN und TALBOYS 1981, MARRÉ 1979, MOREAU und CATESSON 1982, RÜTZE und LIESE 1980, SAVVIN 1980, QUELLETTE 1980, SHINGO 1979, PEARCE und RUTHERFORD 1981 usw.).

Bei den untersuchten Traubeneichen wurden selbst innerhalb eines Baumes verschiedene Tracheenverstopfungen gefunden. Die Verstopfungsraten (in Prozent) der Tracheen im Splintteil durch Thyllen wurden mit Hilfe der 1. Abbildung in Grundtabellen geordnet (Tab. 4). Die Tabellen enthalten Daten bezüglich des Durchmessers der Scheiben, des Alters der Bäume, der untersuchten Gesamt-Tracheenzahl im Splint sowie der Verteilung der Tracheenverstopfungsraten der Segmente im Splint. Die Tabellen zeigen auch die durchschnittlichen Jahrringbreiten in den letzten 10 Jahren.

Nehme man den Durchschnittswert der Tracheenverstopfung bei den Bäumen der Kontrollgebiete als 100%, so wird die Verstopfung bei den "gesunden" Bäumen der der Industrie nahe liegenden Gebiete 341% und bei den "kranken" Bäumen 867%. Diese Daten weisen eindeutig darauf hin, dass in den industrienahen Gebieten selbst die heute noch "gesund" scheinenden Quercus petraea-Bäume bereits potentiell "krank" sind. Die Tracheenverstopfung, wie schon früher darauf hingewiesen wurde (JAKUCS und TÓTH 1984, JAKUCS et al. 1986), kann teils als Folge des Schädigungsvorganges, teils als Verhinderung der eventuellen Regeneration bzw. Heilung betrachtet werden. Sie bedeutet nämlich in der normalen Wasser- und Nährstoffzirkulation eine Hemmung, durch welche ein Stresszustand der Bäume hervorgerufen werden kann.

Die Tracheenverstopfung kann auch in der normalen Jahrringbildung der Bäume Störungen verursachen. Bei den erkrankten Bäumen wird häufig eine grosse Anzahl schmaler Jahrringe ohne Früh- und Spätholz beobachtet, dies

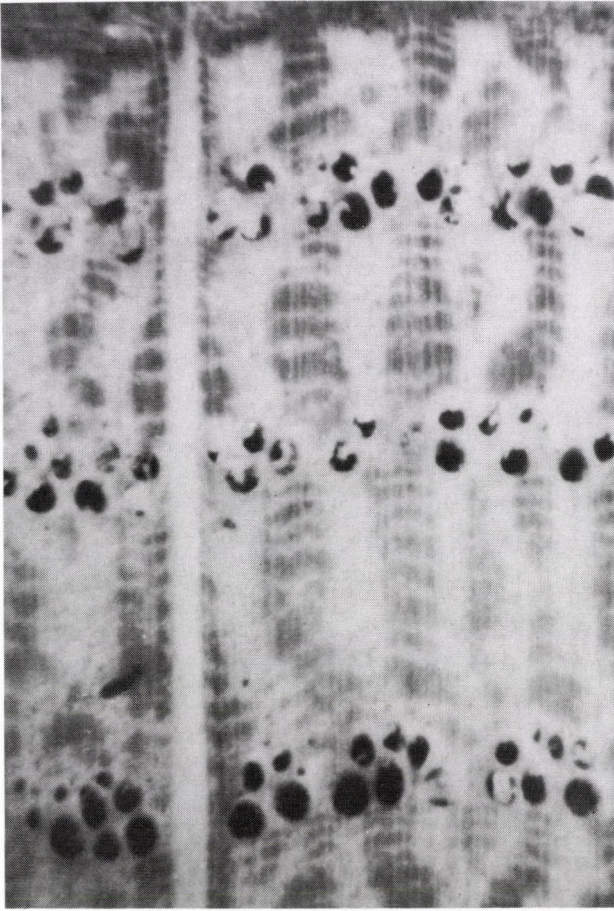


Abb. 6. Normal gewachsene Jahrringe unter der Rinde eines gesunden Baumes
(Foto: JAKUCS P.)

zeigt, dass die geregelten Lebensprozesse der Bäume gestört wurden (siehe Abb. 6. und 7.).

Vergleicht man die gesunden und kranken Proben aus den industriellen Gebieten, so findet man an der gegebenen Stelle immer bei den kranken Bäumen eine grössere Verstopfung. Es kommt sogar vor, dass bei gesunden Bäumen in den luftverschmutzten Gebieten eine grössere Tracheenverstopfung festgestellt wird, als bei den erkrankten Bäumen entfernter liegender Gebiete (so z.B. die Proben 1, 3 und 5 im Vergleich mit den Proben 9 und 7). Diese Tatsache ist auch ein Beweis dafür, dass bei dem Erkrankungs- und

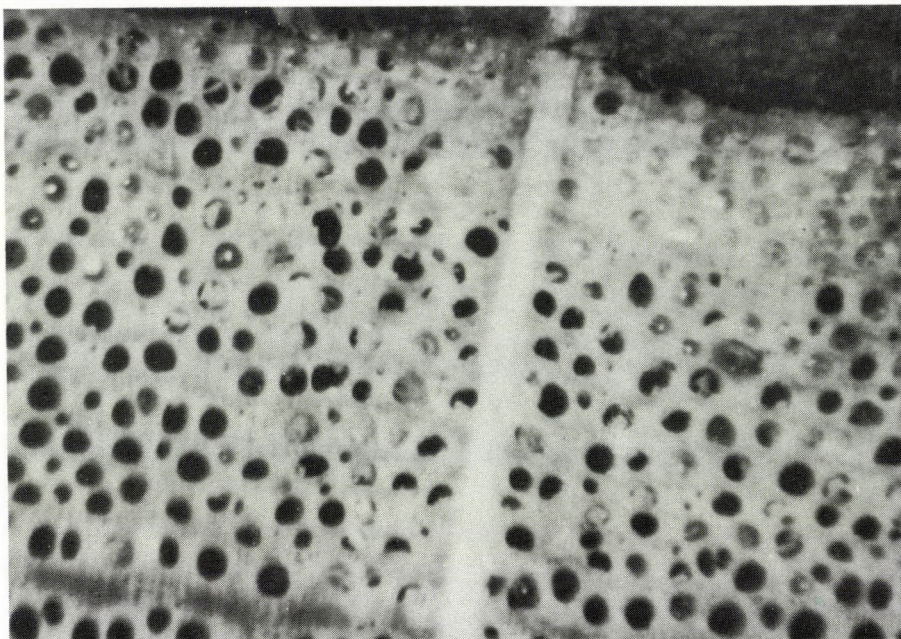


Abb. 7. Jahrringe im unregelmässig gewachsenen Splint unter der Rinde eines kranken Baumes (Foto: JAKUCS P.)

Absterbevorgang der Traubeneichen die Luftschadstoffe primäre Wirkung besitzen.

SCHLUSSFOLGERUNGEN

Die Ursachen für die neuartige Erkrankung und für den Sterbevorgang der Quercus petraea-Bäume in Ungarn sind kompliziert und vielfältig. Es wurde jedoch bereits bewiesen, dass der Ausgangspunkt dieser Vorgänge in der Wirkung der Luftschadstoffe auf den Boden zu suchen ist. Die früheren und die vorliegenden komplexen Untersuchungen in Ungarn erwiesen, dass durch Einwirken der Luftschadstoffe in den vergangenen 10 bis 15 Jahren auch die Parabraunerde in unseren Eichenwäldern stark sauer wurde (JAKUCS 1985, JAKUCS et al. 1986, STEFANOVITS 1986, BERKI 1987, BERKI und HOLES 1988). Demzufolge änderte sich die Pufferkapazität der Böden, wobei die für die Lebewesen toxischen Elemente, Schwermetalle (z.B. Aluminium, Mangan, Eisen, Blei) im Boden wasserlöslich und dadurch aufnehmbar werden. Diese Elemente zerstören die symbiotischen Mykorrhiza-Beziehungen der Wurzeln und gleich-

zeitig wird auch das zur Wasser- und Nährstoffaufnahme dienende Nebenwurzelwerk geschädigt (Details siehe JAKUCS u. Mitarb. 1986).

Die toxischen Stoffe und die Bodenluft können teilweise in die Tracheen gelangen (MEYER 1987) und die Pflanze reagiert auf die Fremdstoffe mit Thyllenbildung. Die Nährstoffe, die pflanzlichen Hormone und andere Regelverbindungen können dadurch nur vermindert oder gar nicht zu den Blättern transportiert werden. Die Photosynthese des Baumes mit gestörter Ökophysiologie wird schwächer, die Bildung der zu speichernden organischen Stoffe verlangsamt sich und die Jahrringe werden schmaler. Die verminderte Wasser- und Nährstoffkapazität zeigt sich in der niedrigeren Tracheenzahl der grünen Sprosse, in den kleineren Stomagrößen sowie in der verminderten Stomazahl (BABOS 1987).

Das endgültige Absterben der Bäume kann ein rascher oder aber ein sich jahrelang hinziehender Vorgang sein. Darin spielen wahrscheinlich sowohl die lokale Akkumulation im Boden oder der Synergismus der Wirkfaktoren, als auch die individuell grössere oder kleinere Toleranz der Bäume eine Rolle. Auf alle Fälle werden Vorhandensein und Entwicklung der Krankheit neben mehreren anderen Symptomen in der Verminderung der Jahrringbreiten sowie im Zuwachs der Tracheenverstopfungen gezeigt.

Unsere Untersuchungsdaten bewiesen, dass diese Vorgänge im Umkreis industrieller Betriebe mit hoher Luftschadstoffemission ausgeprägter und rascher ablaufen. Sie zeigen sich ferner nicht nur im endgültigen Absterben der Bäume, sondern auch in der bedeutenden Verminderung der Holzproduktion der heute noch stehenden und "gesund" scheinenden Exemplare.

LITERATUR

- Babos, K. (1987): Vergleichende Gewebeuntersuchungen der kranken und gesunden Quercus petraea-Stämme (ungarisch). Bot. Közlem., (im Druck).
- Babos, K., Martonos, K.I. (1985): Investigations on the wood of ill sessile oaks (in Hungarian). Az Erdő, 34: 24–28.
- Beckman, C.H., Talboys, P.W. (1981): Anatomy of resistance. In Mace, M.E., Bell, A.A., Beckman, C.H. (eds): Fungal Wilt Diseases of Plants. Acad. Press, New York, p. 431–521.
- Berki, I. (1987): Veränderungen einiger chemischer Parameter des Bodens innerhalb von 10 Jahren in der Parabraunerde beim "Síkfőkút Project". Acta Biol. Debrecina, (im Druck).
- Berki, I., Holes, L. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn II. Elementkonzentration in Blättern der gesunden und kranken Bäumen sowie in Böden. Acta Bot. Hung., 34: 25–37.

- Holes, L., Berki, I. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn III. Gestaltung des Nebenwurzelwerkes und der Mykorrhiza-Verhältnisse bei gesunden und kranken Bäumen. Acta Bot. Hung., 34: 39-49.
- Jacobi, W.R., McDonald, W. (1980): Colonization of resistant and susceptible oaks by Ceratocystis fagacearum. Phytopathologia, 70: 608-623.
- Igmándy, Z., Traser, Gy., Varga, F., Vasas, E. (1986): Jahrringanalysen abgestorbener Traubeneichenstämme (ungarisch). Az Erdő, 35: 457-461.
- Jakucs, P. (1985): Summarizing the trends of element-movement in the forest. In Jakucs, P. (ed.): Ecology of an Oak Forest in Hungary, Results of Síkfőkút Project 1. Akad. Kiadó, Budapest, p. 511-526.
- Jakucs, P., Tóth, J.A. (1984): The filling of sapwood tracheae of ill sessile oaks (in Hungarian). Az Erdő, 33: 348-350.
- Jakucs, P., Mészáros, I., Papp, B.L., Tóth, J.A. (1986): Acidification of soil and decay of sessile oak in the "Síkfőkút Project" area (N-Hungary). Acta Bot. Hung., 32: 303-322.
- Jakucs, P., Berki, I., Holes, L., Tóthmérész, B. (1988): Lokale industrielle Emission und Waldschäden in Nordungarn I. Problemstellung, Ausgangshypothese und zusammenfassende Wertung. Acta Bot. Hung., 34: 11-24.
- Kreml, H. (1984): Saurer Regen und Holzqualität. Holzrundschau, p. 67-70.
- Marré, E. (1979): Fusicoccin: a tool in plant physiology. Ann. Rev. Plant Physiol., 30: 273-288.
- Meyer, H. (1987): Das Wurzelsystem geschädigter Waldbestände. Allg. Forst Zschr., 27/28/29: 754-757.
- Moreau, M., Catesson, A.M. (1982): Nouvelle approche des maladies vasculaires et réflexion sur la spécificité parasitaire. Cryptogamie, Mycologie, 3: 11-31.
- Pearce, R.B., Rutheford, J. (1981): A wound-associated suberized barrier to the spread of decay in the sapwood oak (Quercus robur L.). Physiol. Plant Pathol., 19: 359-369.
- Rütze, M., Liese, W. (1980): Biologie und Bedeutung der amerikanischen Eichenwelke. Mitt. Bundesforschungsanstalt Forest und Holzwirtschaft, Hamburg-Reinbeck, 128: 1-109.
- Quellette, G.B. (1980): Occurrence of thyloses and their ultrastructural differentiation from similarly configured structures in American elm infected by Ceratocystis ulmi. Cand. J. Bot., 58: 1056-1073.
- Shigo, A.L. (1979): Tree decay. An expanded concept. USDA Forest Serv., Agric. Inf. Bull., 419: 1-73.
- Stefanovits, P. (1986): Einige neuere Angaben zur Versauerung der Böden. (Ungarisch). Magyar Tudom., 11: 339-341.
- Szavvin, I.M. (1981): O diagnostike sostoyaniya i ustoychivosti k grinym boleznyam duba. Lesn. Hoz., 10: 57-58.

Gemessene Tracheenverstopfungen des Traubeneichen in Wälder des Industriegebietes Sajó-Tal und der Kontrollgebiete (s. noch JAKUCS et al. 1988)

[illegible]

ADAPTIBILITY OF TREES TO THE CHANGING ENVIRONMENT
(A THEORETICAL APPROACH TO THE POSSIBLE CAUSES OF FOREST DECAY)

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The cause and possible methods of prevention of forest dieback are not clearly defined at the present time. Bearing this in mind I try to discuss the role of some factors rarely considered, but which may also have their effects on forest dieback.

The main question is: why are just the forests dying? It can be stated on the basis of theoretical and practical experience that the tree as a life form is not viable enough in rapidly changing environmental conditions. The morphological features of trees, their long generation time and their dependence on symbiotic organisms, such as ectomycorrhizal fungi ensures them a kind of advantage in natural selection only in slowly changing and even conditions. It seems, however, that the environmental changes are accelerating due to human activity.

It is time we realized that it would require much more effort to make any progress in research investigating the causes of forest dieback and its possible prevention. We are facing a very complex and polyfactorial problem. Consequently, scientists hold different views on it. According to many researchers (ECKSTEIN et al., 1983, FLUEHERL et al., 1981, VINS et al., 1982) environmental pollution, including acid rain can be blamed for the decay of trees, though direct connections were not found between the impact of air pollutants and forest decay.

Several case studies carried out in forests exposed to acidic precipitation can be found in a review by Evans (1984). However, among these papers only one indicated a significant discrepancy between the yields of trees in forests exposed to acidic precipitation and those not affected by this factor (see JONSSON and SUNDBERG, 1972 and also JONSSON, 1977). The other results showed no or very little difference between tree growth in affected areas and that of control stands. Computer simulation models gave similar results. According to MCFEE (1983) the acidification of soils is due

to the several natural processes, such as nitrification, decomposition of organic matter, carbon dioxide resulting from microbial activity, and acidic deposition. He stresses, however, based upon experimental data, that the amount of acidic inputs from the atmosphere have a value of one or two in order of magnificance less, than those originating from everyday farm practice, like N-fertilizing and liming.

As stated by some scientists (BOWEN and MERRILL, 1982; MIELKE et al., 1983; TAINTER and HAM, 1983) the oak wilt in the USA was caused by a fungus called Ceratocystis fagacearum. In another case the death of some oak species also in the USA were due to two successive years of drought (TAINTER et al., 1982). The diseased trees were infected by secunder parasites, mainly by Hypoxylon atropunctatum.

The problem is very similar when the decay of oak forests in Hungary is considered. Several possible causes are mentioned in the Hungarian monthly forestry journal, The Forest (Az Erdő) (August 1984). According to IGMÁNDY et al. (1984) the main causes are pathogen microorganisms. However, JAKUCS (1984) and JAKUCS and TÓTH (1984) put the blame on pollution as the possible main cause. In their papers HANGYÁLNÉ (1984) and VAJNA et al. (1984) suggested that, in spite of having isolated various fungi such as Ceratocystis, Fusarium, Diplodia from dying oak trees, on the basis of previous experience, they do not believe those fungi are the primary causes. SZONTÁGH's work (1984) deals with the role of Green oak tortrix moth, mottled umber and related species in the growing susceptibility of sessile oak to diseases. As stated by MÉSZÁROS (1984) the increasing acidity of soils due to acidic deposition is not harmful as such. The dangerous effects lie with the growing solubility of metals like Al, Fe, Mn and heavy metals in acidic soil solutions, which sometimes reach toxic concentrations.

The debate about oak decay in Hungary first appeared in The Forest (Az Erdő) then continued in the Hungarian scientific journal Hungarian Science (Magyar Tudomány). IGMÁNDY (1985) called this phenomenon an epidemic caused by an Ascomycetes fungus, Ceratocystis piceae. As for JAKUCS (1985) he asserts that the primary sources of the decay are the direct and indirect effects of acidification. His opinion seems to be supported by STEFANOVITS's results (1985), which, however, contradict MCFEE's research (1983). In his paper STEFANOVITS compared the pH values and hidrolitic acidity values of the same soil samples measured first in the late 50-s, early 60-s, then recently. As stated by Stefanovits the results show considerable acidification during the 25-30 year period surveyed. Since

forests have never been treated with fertilizers and it is also improbable that natural soil dynamic processes are responsible for these changes, they may have been caused by deposition from the atmosphere. It also has to be taken into consideration that the rate of decay varies from subspecies to subspecies (BORHIDI, 1986). According to him the most susceptible of all is Quercus petraea ssp. delachampii. A subsequent gradation of insects and a drought period can seriously affect the populations of this subspecies, even causing abrupt wilt and death of the trees.

Based upon the evidence mentioned, SOLYMOS correctly wrote in his introduction (Erdő, 1984): "we can not answer the question yet, as to what has been causing all the damage".

Having no intention to take sides I should like to direct some attention to other factors and phenomena which are rarely mentioned in association with the forest decay.

As stated by DINOOR and ESHED (1984) pathogens live with their host organisms in dynamic equilibrium in their natural habitat. Natural plant populations are heterogenous in most cases. Individual plants of identical species occur in soliters or form clusters, mixed up with individuals of other species. It is the activity of the pathogens by invading and destroying the dense and homogenous stands, which increases diversity. Much evidence supports this hypothesis. According to HARPER (1977) who has analysed other researcher's results "it seems that host-specific pathogens are most successful in communities dominated by one single species". In accordance with his statement he directs attention to the danger of monoculture, though appreciates its advantages. He asserts that producing in monocultures is safe and economical so far as they are devoid of pathogens. When present pathogens can cause serious damage to the population, as it is well-known in the case of Chestnut wilt caused by Endothia parasitica and of Elm-wilt brought about by Ceratocystis ulmi. In HARPER's words: "Diversity in natural communities reflects the defeat of pure associations." Due to the selective pressure caused by pathogens the distance will increase between similar host organisms in a population. This process enables other species to intrude into these gaps causing in this way further diversity. The resistant host organisms inhibit the spread of the propaguli of the parasites. In this way the susceptible genotypes are separated and the drive of selective pressure is also inhibited. However, DINOOR and ESHED (1984) found HARPER's hypothesis unacceptable, because propaguli of the host organisms do not spread so fast as those of the (at least above

ground) pathogens. Nevertheless, it can not be doubted that mixed stands do not further the expansion of pathogens.

Blending of various species and the isolation of individuals of one species must produce agreeable conditions for prevention against parasitic attacks. Diversity exists within one species as well as among different species. The importance of it lies with resistance to pathogens, which becomes evident when they are present. The importance of intraspecific diversity is highlighted by the fact that where self-pollination or vegetative propagation occurs species are much more affected by pathogens than where cross-pollination prevails. In VANDERPLANCK's opinion (in HARPER, 1977) there is no better means to prevent diseases than increasing diversity by means of crossing. According to GREGORIUS et al. (1985) even the susceptibility of trees to pollution is connected with a drop in diversity due to several factors. BORHIDI (1986) also directs attention to diversity in his paper dealing with the decay of sessile oak which affects the three subspecies in different proportions.

As stated by DINOOR and ESHED (1984) when in a state of dynamic balance the disease level is low, the impact of parasites on host organisms is not significant. Epidemic afflicts a community when that balance is disturbed or changed. In such cases single plants can be diseased or even die and the balance will recover later. I think that various forms of pollution or a long-lasting drought period (particularly when they are present at the same time) can be the factors bringing about the changes responsible for the disturbance of the balance. Taking into consideration HARPER's (1977) theory on the role of diversity in resistance to diseases, we can not rule out the possible part that the homogeneity of our forests played in their deterioration. It is highly likely that homogeneity caused a decrease in resistance to biotic and abiotic stresses (e.g.: pollution, drought etc.) as well (see GREGORIUS et al., 1985).

Why have our forest stands become homogenous? This process could have been helped by forests of vegetative origin becoming common, by the increasing number of pure stands and by using various selection methods (selected seeds, further stand selection). Though, the above statement is valid for most of our tree species, the decay has not afflicted all of them yet. This may be partly due to the different genetic properties of different trees and their parasites or to other, mainly abiotic factors. Taking beech (*Fagus sylvatica*) as an example, it is known that this tree grows in our mountainous regions, which are transected by large valleys thus providing

geographical isolation. In the case of beech it is possible, that those fungi, which live in mycorrhizal connection with the tree can better tolerate the high acidity of soils than those of the oak. However, it should be mentioned that there is not much difference between soil pH values in the acidic beech and oak forests. There are certain causes of homogeneity which are of biological origin. It would seem, that the most afflicted tree species (conifers, oak) are all in symbiosis with fungi forming ectomycorrhiza. The effects of micorrhizal fungi on their host plants are described by MOSER and HASELWANDTER (1983). According to them accelerated growth of plants "infected" by such fungi was experienced long ago. It has been reported in several cases that mycorrhiza-forming fungi had a protective effect on their hosts in general and increased their resistance against pathogens. In some instances they have been found to absorb, accumulate and tolerate high concentrations of heavy metals.

It is evident that all the factors affecting the physiological properties of either the fungus or the tree (or both) are capable of changing the whole functional system.

As can be found in several papers on ecology published recently, there have been several changes in our environment which could have had a damaging impact on components of the forest ecosystems (trees, mycorrhizal fungi, and other organisms in the rhizosphere). On the other hand these changes would have helped the living condition of pathogens. The main negative changes are: pollution, drought, and the sometimes very cold winters. What concerns the effects of acidic depositions, there is a very important statement in LOBANOW's work (1960) namely that the ectomycorrhizal fungi of oaks unlike other similar organisms can thrive in alcalic chestnut-brown forest soils. According to it we can assume that the acidification of soils in certain circumstances can have negative effects on these organisms (see: JAKUCS, 1984) thus causing disturbance in the physiological processes of the plants leading ultimately to their weakening. At first sight BORHIDI (1986) would seem to contradict this when writing that Penny Bunn is most abundant in those oak forests where the pH values of the soils are lowest. These stands do not show any sign of disease. However, the impact of acidification is most damaging on calcareous soils turning them acidic. The fungus species occurring on the two types of soils may be different (BORHIDI, personal data).

It is known from EVANS (1984) that organisms having protective cover are not so sensitive to the acidity of precipitation as those without such

cover. For this reason certain kinds of bacteria, other single cell organisms and lichens are very sensitive to changes in pH-values. Prokaryotes are capable of tolerating a narrower pH-range, than multicellular organisms. The bulk of Prokaryotes reach the maximum of their motility between pH 6.8-9.0. Decreasing pH from 7.5 to 5 for example can cause a 50 per cent drop in ciliar motility of Bacillus brevis.

As stated by TRAPPE et al. (1984) the microbes of the rhizosphere have considerable effects on the activity of mycorrhizal fungi. BERTOLDI et al. (1977) carried out research surveying the growth inhibiting effect of a pesticide on onion. The inhibiting effect was due to the impact of the pesticide on soil microbes rather than on mycorrhizal fungi. The pesticide has not had direct effects on the colonizing ability of the mycorrhizal fungus. Lacking direct evidence it may be assumed that the unfavourable changes mentioned earlier (pollution, acid rain, drought) can affect trees not only through their mycorrhizae but by controlling microorganisms in the rhizosphere. Weakening of the fungi forming mycorrhiza and as a result a decrease in their protective role may encourage parasites to intrude. The selective pressure of different forms of pollution, drought and parasites is likely to increase in proportion with the rate of homogeneity of a stand. It also may be assumed that the decay of individual trees sometimes can be a self-generating process. An ailing tree usually seems to develop its above-ground parts at the expense of its root system. (According to WILCOX, 1983, the shoot-system has an advantage when photosynthetic products are distributed.) A relatively less developed root-system, however, can offer less to fungi capable of forming mycorrhizae. The above effects of selective pressure cause a further increase in homogeneity. However trees, which survive have greater resistance against selective environmental factors. In theory a stand after selection could reach the level of diversity desired in slowly changing environment. However, it presumably will not happen in practice due to large-scale human activity which results in fast-changing environmental conditions. A homogenous population or a genetically homogenous species finds it hard to tolerate rapid changes. According to certain experimental findings and theoretical views it is held that the tree as a life form is not viable enough in rapidly changing conditions or at least herbaceous plants are at an evolutionary advantage. It seems that tree prefer longer and more even periods. The larger an organism is the longer an even period it needs. This is exemplified in some respect by prehistoric reptiles.

It is also known that trees appear on sites at the last stage of succession, when conditions are relatively stable. Trees will not occur on a site, where fundamental conditions do not meet their demands as is the case on the spoils of ore mines. KINZEL (1982) wrote that it is generally known that soils containing large quantities of heavy metals are devoid of trees. (However, in contradiction to this is the fact, that trees and shrubs can be found among the dominant plants of serpentine soils. The vegetation of serpentine climax though, will never reach the cover of the climatic climax (BORHIDI, 1988). The difference between the vegetation on serpentine and heavy metal soils may be explained by the oligotrophic feature of the latter.) Regression occurs when environmental changes upset the balance of a climax community as happened during the glacial periods in Europe. Other more recent examples can be also found, such as the natural development of Heide vegetation.

The next question to be raised is, whether there are any other features, apart from the relative inertia of large organisms, which increase the vulnerability of trees to changes. It seems there are many of them. It is known that trees are in direct contact with the atmosphere and soil through their large crowns and root system. In this way they are exposed to the effects of pollution both directly and indirectly. It is also known that trees, like other plants, but unlike other organisms are more exposed to local unfavourable changes, because they are restricted to their growing sites.

There is a considerable difference between the generation time of trees and herbaceous plants — let alone bacteria. Oak for example needs 30–35 years to develop a following generation capable of shedding nut. On the other hand herbaceous plants can complete their life-cycles in one or two years. Ephemerals can have 3–4 generations annually and bacteria need only half an hour to double their number. In my opinion, these features may also result in different adapting capabilities of the organisms, so trees may have a serious disadvantage when rapid environmental changes occur.

Lastly, I would like to mention another factor which can inhibit the evolutionary adaptation of trees. According to the Yugoslav Professor LAKUSIĆ (personal communication) lichens can not be compared with such species as beech (*F. sylvatica*) for example, on theoretical basis, because lichens are forms of biocoenoses. According to him this feature makes lichens much less resistant against pollution than single species are. It should be borne in mind, however, that such an interpretation of lichens is

not mind, however, that such an interpretation of lichens is not new. BORHIDI wrote in 1969: "lichens are in a sense elementary ecosystems which consist of autotrophic and heterotrophic components". LIN WU and KRUCKEBERG (1985) explained the rare occurrence of species of the Fabaceae family on heavy metal soils. As stated by them the complexity of the N-fixing system in these symbiotic plants may make them rather sensitive to the toxicity of heavy metals. They can only be tolerant when both components, i.e. the plant and the bacterium are tolerant. Perhaps the same applies to our decaying trees, because they are also connected to simbiotic organisms, the ectomycorrhizal fungi. Thus the host plant and the fungi forming ectomycorrhiza must have developed in coevolution. Having the two different genomes connected in this manner may involve significant evolutionary disadvantage in rapidly changing living conditions.

I of course dare not state on the basis of this theory, that all the trees on the Earth will soon be eliminated. Lucky and accidental modifications — hopefully great in number — will occur. However, the more flexible and faster spreading herbaceous plants presumably will have a better chance of survive than trees and shrubs.

We could help trees in their fight to survive in this uneven battle using proper environmental management and perhaps, by biotechnological means (selection of cell and tissue cultures). The practices applied in forest management, which might have decreased the diversity of various stands, ought to be also changed in a way which recognises the importance of genetic variety.

Some might dispute the validity of this hypothesis on the ground that not only trees are decaying nowadays. There are several reports of the repression or extinction of criptogam and herbaceous plants from certain sites. In these cases, however, the explanation is much simpler, than in the case of trees. Sometimes the affected species have a low tolerance, with a narrow area spectrum or in some cases are endemic species. The forest decay, in the meantime, afflicts various species with wide areal distribution and has no straightforward explanation.

LAURENCE and WEINSTEIN (1981) suggested that plants affected by air pollutants can easily be attacked by parasites. If pollution really played an important role in forest decay, than we are facing a vexed question, since we know almost nothing about the effects of pollutants on arable crops and trees. It also should be borne in mind that as DINUS (1974) stated: "exploitation of natural plant communities by man causes irreversible

changes in their structure". These changes may upset the balance of a community and serious epidemics can break out caused by earlier local and unimportant pathogens, such as rust fungi in a pine forest in the Southern USA (DINUS, 1974). So we can not leave out of consideration the seemingly harmless pathogens in a community. Hopefully in the future we will be able to identify the roles of different factors in forest decay. It is very important to know, whether pollution or parasites can be blamed, because in the latter case we can hope that a balance develops between hosts and parasites sooner or later. If pollution is the dominant factor and parasites are secondary causes as is widely held than we have the prospect of a bleak future without tress.

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REFERENCES

- Beckman, C.H., Kuntz, J.E., Riker, A.J., Berbee, J.G. (1953): Host reponses associated with the development of oak wilt. Phytopathology 43: 448-454.
- Bertolidi, M. de, Giovannetti, M., Griselli, M., Rambelli, A. (1977): Effects of soil applications of benomyl and captan on the growth of onions and the occurrence of endophytic mycorrhizas and rhizosphere microbes. Ann. Appl. biol. 86: 111-115.
- Béky, A. (1984): The health condition of the sessile oak in experimental forest managing and timber production areas (in Hungarian). Az Erdő 119: 351-352.
- Borhidi, A. (1969). Plant and Environment. In Kárpáti, Z. (ed.): The World of plants II. (in Hungarian). Gondolat Könyvkiadó, Budapest.
- Borhidi, A. (1986): Oak dyebark — epidemic or acidification? (in Hungarian). Magyar Tudomány 31: 368-373.
- Borhidi, A. (1988): El efecto ecológico de la roca serpentina sobre la flora y vegetación de Cuba. Acta Bot. Hung. 34: 123-174.
- Borhidi, A. (1989): Phytogeography and Vegetation Ecology of Cuba. Akadémiai Kiadó, Budapest (in print).
- Bowen, K.L., Merrill, W. (1982): Oak wilt (*Ceratocystis fagacearum*) foci related to ridge bearing and aspect in Pennsylvania, USA. Plant Dis. 66: 137-139.

- Dinoor, A., Eshed, N. (1984): The role and importance of pathogens in natural plant communities. Ann. Rev. Phytopathol. 22: 443-466.
- Dinus, R.J. (1974): Knowledge about natural ecosystems as a guide to disease control in managed forests. Proc. Am. Phytopathol. Soc. 1: 184-190.
- Eckstein, D., Aniol, R., Bauch, J. (1983): Dendroclimatological investigations on fir (*Abies alba*) dieback. Eur. J. For. Pathol. 13: 279-288.
- Evans, L.S. (1984): Acidic precipitation effects on terrestrial vegetation. Ann. Rev. Phytopathol. 22: 397-420.
- Fenn, P., Durbin, R.D., Kuntz, J.E. (1975): Wilt development in red oak seedlings: a new system for studying oak wilt. Phytopathology 65: 1381-1386.
- Flueherl, H., Kienast, F., Scherrer, H.U., Dester, B., Polonski, J., Keller, T., Schwager, H., Schweingruber, F.H., Mahrer, F., Blaser, P. (1981): Assessment of forest damage and air pollution in the Rhone Valley (Switzerland). EIDG Anst. Forstl. Versuchswes. Mitt. 57: 358-500.
- Gregorius, H.-R., Hattemer, H.H., Bergmann, F., Müller-Starck, G. (1985): Umweltbelastung und Anpassungsfähigkeit von Baumpopulationen. Silvae Genetica 34: 230-241.
- Hangyálné, B.W. (1984): Mycological studies related to the oak dyebark (in Hungarian). Az Erdő 119: 359-361.
- Harper, J.L. (1977): Population Biology of Plants. Academic Press, London.
- Igmándy, Z., Pagony, H., Szontagh, P., Varga, F. (1984): Survey on the dyebark occurred in our sessile oak forests (1978-1983) (in Hungarian). Az Erdő 119: 334-341.
- Igmándy, Z. (1985): The dyebark of the sessile oak in Hungary. (in Hungarian). Magyar Tudomány 30: 456-459.
- Jakucs, P. (1984): Ecological explication of the dyebark of the sessile oak forests (in Hungarian). Az Erdő 119: 342-344.
- Jakucs, P. (1984): Preliminary report about the research theme "Complex study of terrestrial natural and modified ecosystems in the Síkfő-kút Project area and its surroundings" according to the stage in September, 1984 (in Hungarian). KLTE, Ökológiai Tanszék, Debrecen.
- Jakucs, P., Tóth, J.A. (1984): Tapping of the vascular tracheas in sick sessile oaks (in Hungarian). Az Erdő 119: 348-350.
- Jakucs, P. (1985): The effect of the intensifying acidification on to natural living world (in Hungarian). Magyar Tudomány 30: 731-741.
- Jonsson, B., Sundberg, R. (1972): Has the acidification by atomospheric pollution caused a growth reduction in Swedish forests? A comparison of growth between regions with different soil properties. In Bolin, B. (ed.): Supporting Studies to Air Pollution Across National Boundaries. The Sweden's case study for the United Nations Conference on the Human Environment. Royal Ministry of Foreign Affairs, Royal Ministry of Agriculture, Stockholm. 46 p.
- Jonsson, B. (1977): Soil acidification by atmospheric pollution and forest growth. Water, Air, Soil Pollut. 7: 497-501.
- Kinzel, H. (1982): Pflanzenökologie und Mineralstoffwechsel. Verlag Eugen Ulmer, Stuttgart.

- Laurence, J.A., Weinstein, L.H. (1981): Effects of air pollutants on plant productivity. Ann. Rev. Phytopathol. 19: 257-271.
- Lin Wu, Kruckeberg, A.L. (1985): Copper tolerance in two legume species from a copper mine habitat. New Phytol. 99: 565-570.
- Lobanow, N.W. (1960): Mykotrophie der Holzpflanzen. VEB Deut. Wiss., Berlin.
- McFee, W.W. (1983): Sensitivity ratings of soils to acid deposition: A review. Env. Exp. Bot. 23: 203-210.
- Meyer, F.H. (1974): Physiology of Mycorrhiza. Ann. Rev. Plant Physiol. 25: 567-586.
- Mészáros, L.I. (1984): Comparative chemical analysis of the soil, root and leaf (in Hungarian). Az Erdő 119: 367-369.
- Mielke, M.E., Haynes, C., Rexrode, C.O. (1983): Local spread of oak wilt in north-eastern West Virginia (USA) during 1970-1982. Plant Dis. 67: 1222-1223.
- Moser, M., Haselwandter, K. (1983): Ecophysiology of mycorrhizal symbioses. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological plant ecology III. Encyclopedia of plant physiology. New series. vol. 12C. Springer-Verlag, Berlin-Heidelberg-New York.
- Parmeter, J.R., Kuntz, J.E., Riker, A.J. (1956): Oak wilt development in bur oaks. Phytopathology 46: 423-436.
- Solymos, R. (1984): The health condition of our forests (in Hungarian). Az Erdő 119: 333 p.
- Stafnovits, P. (1986): Some new data about the acidification of soils (in Hungarian). Magyar Tudomány 31: 339-341.
- Struckmeyer, B.E., Beckman, C.H., Kuntz, J.E., Riker, A.J. (1954): Plugging of vessels by tyloses and gums in wilting oaks. Phytopathology 44: 148-153.
- Szontágh, P. (1984): The damage caused by phyllophagous insects of the oak in the years 1962-1981 (in Hungarian). Az Erdő 119: 353-358.
- Tainter, F.H., Ham, D.L. (1983): The survival of *Ceratocystis fagacearum* in South Carolina (USA). Eur. J. For. Pathol. 13: 102-109.
- Tainter, F.H., Williams, T.M., Cody, J.B. (1982): Drought as a cause of oak decline and mortality on the South Carolina coast. Phytopathology 72: 958 p.
- Trappe, J.M., Molina, R., Castellano, M. (1984). Reactions of mycorrhizal fungi and mycorrhiza formation to pesticides. Ann. Rev. Phytopathol. 22: 331-359.
- Vajna, L., Eke, I., Csete, S. (1984): Mycological-phytopathological investigations related to the dieback of sessile oak forest stands (in Hungarian). Az Erdő 119: 362-366.
- Vins, B., Pospisil, F., Kučera, J. (1982): Evaluation of development of emission damages in the protected landscape area of the Jizerske Mountains, Czechoslovakia. Lesnictví (Prague) 28: 87-102.
- Wilcox, H.E. (1983): Fungal parasitism of woody plant roots from mycorrhizal relationships to plant disease. Plant Disease 21: 221-242.

SEED BANK IN THE SOIL AND ITS ROLE DURING SECONDARY SUCCESSIONS INDUCED BY
SOME HERBICIDES IN A PERENNIAL GRASSLAND COMMUNITY

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The seed bank in the soil of an old perennial grassland community (*Pulsatillo-Festucetum rupicolae*) was studied in order to provide a basis for a better understanding of the background of floristic and population level changes during secondary succession induced by leaf herbicides.

The procedure used in this study was not designed to provide a complete assessment of the size and composition of the seed bank. The main purpose of this investigation was merely to detect the presence of a persistent seed bank in the intact community and to recognize the changes of species composition of seeds in the soil during primary and secondary succession. It was attempted to assess the role of the seed bank in vegetation dynamics, as well as the effect of vegetation, developed after the herbicide treatments, on the composition of the seed banks.

The method of MALONE (1967) was applied to separate the seeds from the soil. The seeds were counted under a binocular stereo-microscope. To determine the viability of seeds, ZELENCHUK's (1961) technique for estimating the "apparently viable" seeds was chosen.

It was concluded that the seed bank of the old semi-natural grassland community near the stable state was relatively small and most of the seeds seemed to be short-lived in the soil. A feature of the results was the lack of correspondence between the species composition of the seed flora and that of the associated vegetation. In general, the seed bank was less diverse than the vegetation from which it was derived. There were several species in the vegetation which were completely absent from the seed bank or were represented by very few seeds. Nevertheless, it was striking that many of the species that could be considered very rare or less frequent in the vegetation made a large contribution to the seed bank. Species with these minute seeds, dominant in the soil, were as follows: *Rumex acetosella*, *Silene otites* ssp. *hungarica*, *Potentilla argentea* and *Fragaria viridis*.

The role of seed banks in the response of vegetation after disturbance was very small. Vegetative regeneration could be considered as the most important factor in the rapid recovery. Comparison between the present vegetation formed after the selective-herbicide sprayings and the seed bank also revealed a strong difference.

During secondary succession after the total destruction of the vegetation the species number in the seed bank was nearly the same

as in the intact community. Nevertheless, the initial floristic composition did not reflect "well" the composition of the seed bank. At the beginning of the succession there were several species in the community, whose seeds were completely absent from the seed bank, but their dominance — abundance in the standing vegetation was very strong. This observation also indicated that the colonization of the bare ground proceeded not only from the seeds. The total number of species in the soil slightly changed, but the species composition had altered markedly during the 4 years studied. The seed content was the smallest at the very beginning of the succession (seed input was small; a high proportion of the species was not able to reach the stage of producing seeds) and reached the maximum value in the following year, then showed a declining tendency in the course of secondary succession.

During primary succession on sterilized soil the species number of seed bank increased within the 4 years studied. By the second year the seed content had multiplied by 5 and after this maximum it showed a continuous decrease in spite of the increase of species number.

INTRODUCTION

The knowledge of viable seed content in the soil is essential in the study of population and vegetation dynamical processes, as well as in examining the regeneration capability of plant communities.

It has been commonly observed that in undisturbed; old grassland communities there is a relatively small seed bank. Many of the species present in the aboveground vegetation are absent from the seed bank. There is no close correspondence between the species composition of the seed bank and the associated vegetation (HAYASHI and NUMATA 1971, THOMPSON and GRIME 1979, THOMPSON 1986, JERLING 1983). The ecological and physiological background of this evidence was revealed and discussed by THOMPSON and GRIME (1979) and THOMPSON et al. (1977).

According to GRIME (1979), in grasslands the species composition of seed bank, primarily the presence of the seeds of grasses is of greater importance than the total number of the seeds present. GRIME also emphasized that although the seeds of grasses often account for a considerable percentage of the total, their contribution to the seed bank is usually small or negligible except in dry summer. In semi-arid areas the majority of the seeds of grasses germinate in autumn and a large number of seedlings appear on bare ground formed in the dry season. It is true of both annual and perennial grasses.

The regeneration of grasslands is relatively slow after perturbation

or man-induced disturbance. It may be accounted for by the small seed banks and the fact that grassland recovery is mostly determined by vegetative regeneration.

Some authors have also investigated the changes in the seed bank during the secondary succession of grasslands, but the results obtained are insufficient for a reliable interpretation. OOSTING and HUMPREYS (1940) and later DONELAN and THOMPSON (1980) recognized a decline in the total number of seeds in the soil, whereas LIVINGSTON and ALLESSIO (1968) did not detect any trend in an old field succession. In Hungary, no study of buried seeds in relation to succession has been carried out.

The present study examines the seed bank of an old semi-natural perennial grassland community to provide a basis for the analysis of compositional changes during secondary succession induced by some herbicides. This project is a part of an experimental program started in 1979 at the southern foot of the Bükk Mountains (NE Hungary) in a species rich secondary steppe-meadow community (Pulsatillo-Festucetum rupicolae).

In a homogeneous stand of this relatively undisturbed community some leaf-herbicides, selective to dicots or monocots, as well as herbicides of total effect were applied to induce vegetation dynamical processes after disturbance. The studies aim mainly at the understanding of structural changes and regeneration processes of the community. The results, however, cannot be interpreted adequately without information on the population biological behavior of the constituent species.

The reproductive feature of the species, expressed in terms of the number of buried viable seeds, provided fundamental information for the study of vegetation dynamics including regeneration. The data obtained on seed banks in the soil were very useful in analyzing vegetation response to different herbicide treatments and in developing hypotheses on the role of seed reservoir during primary and secondary succession.

The sampling procedure used did not give a complete assessment of seed bank size (for details see later!). That is why this study was considered as an initial attempt designed to evaluate the changes in the seed bank after treatment with herbicides and to compare the seed banks of the treated and non-treated communities. We did not want, however, to compare our results with those of other studies in which complete enumeration of the seeds was the principal aim. This study examines the following problems:

— What is the agreement between the composition of seed bank in the control untreated quadrats and in the aboveground species composition?

- What changes can be detected in the seed bank after applying selective herbicides?
- Does the seed bank contain seeds grasses 1-2 years after killing all monocots while the grasses are completely absent in the vegetation?
- Can the seeds of dicots be found at all in the soil and what similarity can be recognized between the abundance of dicots in the soil and in the vegetation when all dicots were destroyed from the quadrats one year before the determination of seed bank?
- What is the influence of the modified aboveground floristic composition and the vegetatively propagated monocots on the germination of dicotyledonous seeds?
- What is the role of the seed bank in forming the initial floristic composition during secondary succession after destroying all the vegetation?
- How do the composition and size of the seed bank change during the 4 years studied?
- To what extent can the biological features of the first colonizers be responsible for determining the changes in the seed bank?
- How does the seed content in the soil change during primary succession?
- How is the primary succession on sterilized soil taking place?

SEED BANKS IN THE SOIL: A BRIEF REVIEW

Definition

The term "seed bank" which has been widely adopted in recent years means the reserves of viable seeds present in the soil and on its surface.

Seed bank types

In grassland communities, four types of seed banks have been distinguished and described by THOMPSON and GRIME (1979).

In a transient seed bank the seed output cannot be viable in the habitat for more than a year. A subtype included in this group and existing during summer is constituted mainly by a number of annual and perennial common grasses which release their seeds late spring and summer and germinate nearly simultaneously in the cooler moist autumn conditions. The species with transient seed bank have no dormancy mechanism but their ability to germinate over a wide range of temperature and light conditions

facilitates rapid germination soon after seed fall. This type of seed bank provides a regenerative mechanism for population of established plants.

The second major group of species which possess transient seed banks during winter is represented by species that germinate late winter or early spring after winter dormancy. This seed bank type represents a specific adaptation—delaying germination until the beginning of the growing season.

In GRIME's classification two other types of seed banks belong to the persistent seed bank types, in which the component seeds are more than one year old. Seed bank type 3 is characteristic of species whose most seeds germinate in autumn while a smaller proportion becomes buried and persistent in the soil.

Species of type 4 maintain a large persistent seed bank, the size of which changes little over seasons. The seeds of the species belonging to this group cannot germinate immediately after dispersal and germination of seeds may be restricted to the temperature and light conditions. The buried seeds of the great majority of these species retain their viability in the soil for a long time (some decades).

The species with transient seed banks exploit the gaps created by seasonally predictable damage and mortality in the vegetation, while the persistent seed bank confers the potential for regeneration in circumstances where disturbance of the vegetation is temporally and/or spatially unpredictable.

In temperate forests NAKAGOSHI (1985) recognized three types of seed banks of the main constituting species: no reserve of seeds in the growth season (Type I), reduced seed bank (Type II) and permanent seed bank (Type III). Later 9 groups were characterized based principally on the different seed banks and life forms of species. These seed bank categories were considered mainly in ecological studies on the seeds of component species of plant communities.

The role and importance of seed banks

Seed banks in the soil are of great importance in the study of life-cycles of plant individuals, regeneration strategies, demography of plant populations and vegetation dynamical processes in communities.

The quantity and quality of seed banks can be determined by several factors, such as: 1) reproductive potential of plants, 2) dispersal mechanisms, 3) dormancy patterns, 4) soil characteristics, 5) biotic

influences e.g.; predation and decomposition, 6) weather fluctuations and 7) disturbances of the soil surface.

Some of the most important characteristics of the populations reproducing primarily by seeds are the capability of plant individuals determining the seed production and the adaptive capability of the species which can define the period while the seeds retain their viability in the soil. The latter property can mean a survival mechanism for a given population at the same time. Seed banks have therefore a great significance in the maintenance of populations and can also act as a genetic stabilizer when the number of individuals fluctuates. Hard-coatedness of seeds, which is mainly the characteristic feature of annuals (CZIMBER and REITER 1970, CZIMBER 1970a), can also guarantee the fitness of species.

The buried seed population has great significance in plant demography and vegetation development since it is regarded as the potential or initial coenopopulation (initial floristic factor: EGLER 1954, RABOTNOV 1969) which can also determine the direction of further vegetation changes.

The knowledge of seed banks is essential in studying the regeneration capability of communities and in understanding vegetation response to disturbance. In the colonization of disturbed areas the seed bank is the basic source (KEELEY 1977, van der VALK and DAVIS 1978, BARTOLOME 1979, THOMPSON and GRIME 1979, HOPKINS and GRAHAM 1984, COOK 1980, OOSTING and HUMPHREYS 1940, ERICSON 1977). Disturbance of soil often stimulates germination of buried seeds, that is why the role of seed banks is less important in the lack of disturbance. The results of seed bank studies are very useful for predicting the changes during secondary succession. Seeds in the soil may be long-lived. If we know the viability of seeds in the soil and the necessary requirements for germination, useful information on past history of communities can also be obtained (ROBERTS and DAWKINS 1967, HOPKINS and GRAHAM 1983).

The practical significance of seed bank studies is also great. In arable cultivation the presence of large numbers of seeds means that there is a continuing need for weed control (BARCSÁK 1968, CZIMBER and REITER 1970, JENSEN 1969, ROBERTS 1981, ROBERTS and CHANCELLOR 1986). Here the objective is to maintain the seed bank at the lowest feasible level in order to minimize interference with crop production. Seed bank studies can make a contribution to improving the efficiency of crop production and the data obtained on the species composition of arable seed banks can be used

predictively to give guidance on the choice of cultivated plants and of herbicides to be applied for the next year.

The investigation of seed banks in grasslands is especially useful when the swards are renewed. Since the persistent seed banks of the less-desirable grasses contribute to sward deterioration, while at the same time reserves of seeds of leguminous species are valuable in the maintenance of pastures, especially in regions subject to drought.

Seed bank studies

In the past 60 years numerous seed bank studies were carried out in different vegetation types and habitats. As a result of these investigations a vast amount of data has been available from tropical rainforest and taiga, as well as from deserts, semi-deserts, grasslands, prairies, savannas and steppe-vegetation. The results and purposes of seed bank studies have been reviewed by several authors, e.g.; RABOTNOV (1978) and ROBERTS (1981).

The majority of investigations of seed banks are concerned with different meadow and pasture types (CHIPPINDALE and MILTON 1934, DORE and RAYMOND 1942, PRINCE and HODGDON 1946, CHAMPNESS and MORRIS 1948, MILTON 1948, FOERSTER 1956, ZELENCHUK 1961, GOLUBEVA 1962). Most of these early investigations reviewed by MAJOR and PYOTT (1966) and RABOTNOV (1969) were devoted to assess the seed contents (mainly quantity of weed seeds). It was only in the past two decades that the investigations of seed banks in relation to succession and regeneration processes came into the focus (HAYASHI and NUMATA 1968, 1971, DONELAN and THOMPSON 1980, JERLING 1983, BELSKY 1986).

The role of ecological features and life strategies of seeds forming different seed bank types was emphasized by NUMATA et al. (1964), HAYASHI and NUMATA (1971), GRIME (1977), THOMPSON and GRIME (1979), HOWE and CHANCELLOR (1983). Nowadays these investigations have to constitute an integral part in studies of population demography and vegetation dynamics.

In Hungary relatively little attention has been paid to seed bank studies and their ecological perspectives. BENCZE's publication (1963) can be considered as a pioneer work in which one of the techniques for determining weed seed populations was described and the content of buried weed seeds in arable fields was well documented. MÁTHÉ and PRÉCSÉNYI (1971) analyzed seasonal and annual changes in the quantity of weed seeds of the soil in different pastures and cultivated areas. BARCSÁK (1968) estimated the changes of seed bank size mainly in the pastures and induced by grazing of

various intensity. CZIMBER and REITER (1970), as well as CZIMBER (1970b) investigated the resistance of hard-coated seeds of Convolvulus arvensis and Ononis spinosa to various herbicides and the role of these seeds in the reappearance of weeds in arable lands treated by herbicides. Recently, seed bank studies have been carried out only in order to control the content of weed seed populations and the consequences of different cultivations, sward-improving techniques. Little is known about the composition and size of seed banks and the role of viable seeds in the soil in natural plant communities. There is no investigation analyzing seed banks in connection with vegetation dynamics.

MATERIAL AND METHODS

Site description

The field work carried out on a dry-situated hill, at the southern foot of the Bükk Mountains (NE Hungary), at an elevation of about 200–300 m above sea level. The subcontinental climate of this gentle hilly country represents an intermediate position between that of the Great Hungarian Plain and the mountainous region. The mean annual temperature is 9°C, the annual precipitation is about 600 mm. The soil is brown forest soil of csernozom character, formed on loess (see VIRÁGH 1982).

The area, on which our experiment was set, is a secondary steppe community (Pulsatillo-Festucetum rupicolae) near stable state and formed very long time ago following a deforestation. It can be considered as a final stage (subclimax community) in a successional series of grasslands in the given area.

Flora of the study area

The investigated grassland community is rich in species (80–100) and less weedy. Dominant monocots constituting the community are Anthoxanthum odoratum, Agrostis canina and Festuca rupicola. The most abundant dicots are: Achillea collina, Dianthus pontederiae, Genista tinctoria, Hieracium pilosella, Hypericum perforatum, Potentilla arenaria, Pulsatilla nigricans and Thymus marschallianus.

Due to the anthropogenic effects, intensive grazing and trampling, the Festuca pseudovina type of the association, considerably tainted also with weeds, occurs. Besides, agricultural areas, plough-lands and orchards can also be found in the environs. A detailed description of the community studied, the sources of species richness in flora and the reason of the coexistence of many different flora-elements in the area are presented by VIRÁGH (1982) and VIRÁGH and FEKETE (1984). These papers also contain species lists and phytosociological tables of presence-absence and percentage cover scores of species in the investigated permanent quadrats and in the different vegetation types and associations occurring in the immediate vicinity. For illustration the species list of the quadrats selected for the studies with indication of percentage frequency is presented in Table 1,

which characterizes the original state of the stand in June 1979 before spraying and provides basic information for studying of seed banks.

Table 1
List of species

Name of species	Frequency ⁺ %
<u>Gramineae</u>	
Agrostis canina	65.84
Anthoxanthum odoratum	48.96
Bothriochloa (Andropogon) ischaemum	34.32
Briza media	5.52
Bromus mollis	2.40
Chrysopogon gryllus	8.96
Danthonia alpina	11.44
Danthonia decumbens	5.92
Festuca rupicola	81.28
Festuca pseudovina	
Koeleria cristata	6.64
Stipa capillata	0.24
<u>Other Monocotyledons</u>	
Anthericum ramosum	1.68
Asparagus officinalis	0.40
Carex caryophylla	46.00
Luzula campestris	66.64
<u>Dicotyledons</u>	
Achillea collina	87.12
Ajuga genevensis	2.80
Arenaria graminifolia	0.14
Arenaria serpyllifolia	0.16
Asperula cynanchica	14.48
Campanula rotundifolia	0.16
Carlina vulgaris	29.04
Centaurea pannonica	5.44
Centaureum erythraea	1.92
Cerastium brachypetalum	8.88
Chondrilla juncea	0.16
Convolvulus arvensis	1.04
Crataegus monogyna	0.24
Dianthus pottederae	19.28
Dorycnium herbaceum	1.12
Echium vulgare	0.32
Erigeron canadensis	0.16
Eryngium campestre	12.80
Euphorbia cyparissias	35.04
Euphrasia tatarica	30.00
Filipendula vulgaris	15.44
Fragaria viridis	10.16
Galium verum	1.28

Name of species	Frequency ⁺ %
<i>Genista tinctoria</i>	33.76
<i>Hieracium pilosella</i>	29.68
<i>Hieracium bauginii</i>	14.64
<i>Hypericum perforatum</i>	17.92
<i>Inula britannica</i>	2.00
<i>Leontodon hispidus</i>	50.00
<i>Leucanthemum vulgare</i>	0.88
<i>Lotus corniculatus</i>	0.80
<i>Myosotis stricta</i>	1.12
<i>Ononis spinosa</i>	0.32
<i>Orchis morio</i>	0.96
<i>Pimpinella saxifraga</i>	7.36
<i>Plantago lanceolata</i>	29.04
<i>Plantago media</i>	2.32
<i>Polygala comosa</i>	2.40
<i>Potentilla arenaria</i>	42.56
<i>Potentilla argentea</i>	2.40
<i>Pulsatilla nigricans</i>	14.00
<i>Prunella laciniata</i>	2.40
<i>Prunus spinosa</i>	0.16
<i>Rosa canina</i>	0.16
<i>Rumex acetosella</i>	32.64
<i>Rumex thyrsiflorus</i>	0.72
<i>Salvia pratensis</i>	1.12
<i>Saxifraga bulbifera</i>	7.20
<i>Scabiosa ochroleuca</i>	14.48
<i>Senecio jakobaea</i>	0.32
<i>Seseli annuum</i>	24.72
<i>Silene otites</i>	5.52
<i>Silene pseudotites</i>	1.10
<i>Stellaria graminea</i>	2.24
<i>Taraxacum officinalis</i>	1.44
<i>Teucrium chamaedrys</i>	9.44
<i>Thesium ramosum</i>	1.84
<i>Thlaspi jankae</i>	0.32
<i>Thymus marschallianus</i>	92.72
<i>Trifolium alpestre</i>	2.72
<i>Trifolium campestre</i>	0.24
<i>Trifolium pratense</i>	2.24
<i>Trifolium montanum</i>	1.28
<i>Trifolium ochroleucum</i>	0.28
<i>Verbascum phoeniceum</i>	4.72
<i>Veronica dentata</i>	2.48
<i>Veronica hederifolia</i>	0.16
<i>Veronica serpyllifolia</i>	3.12
<i>Veronica spicata</i>	9.66
<i>Viola arenaria</i>	5.60
<i>Viscaria vulgaris</i>	13.52

⁺Frequency percentage was calculated on the basis of the presence of species, in 1250 subquadrats of 20 x 20 cm²

Field experiments (chemical treatments)

The research program was launched in 1979 and ran for 5-6 years in the old grassland community. Some herbicides selective to dicots and monocots and others of total effect were used in order to study secondary succession and regeneration. The chemical composition and doses applied, the action mechanism of leaf-herbicides, and dates of spraying and recording are shown in Table 2. The herbicides used have been widely applied in Hungary mainly in the sward farming for weed control and improvement of the sward (selective extirpation), as well as for destroying the vegetation totally in order to re-sow the sward.

It must be emphasized that every herbicide belongs to the group of leaf-herbicides. They damage only the living plants existing at the time of spraying but the seeds in the soil remain intact. Disturbance in soil surface was not induced by the herbicides.

The action of different leaf-herbicides was sudden and rather short, but the changes induced by herbicides at the community level lasted for a long time after spraying. It must be noted that during the period of the 5 years studied there was no succession in the general sense of the word, in the sense of substitution of "well-defined" communities by others ("macro-succession"). Indeed species previously present in the original community reappeared. Different regeneration processes, local secondary succession of "coenostates" ("micro-steps") after herbicide treatments (disturbance) were initiated and studied in permanent quadrats.

Five kinds of experiments were connected with the seed bank studies. For a better understanding of the seed bank results it is necessary to summarize the main features of the experiments and the main conclusions obtained on the aboveground floristical changes.

Control experiment

It represents vegetational changes without any treatment. Expression of seasonality and the strong effect of the differences between years were well detected. Dynamically stable state of the intact community and its great resistance against drought but small resilience referring e.g. to the degree of its recovery following disturbance were well demonstrated.

Gabonil 7 experiment

The dicots, the less dominant group, were removed. Immediately after spraying the monocots became dominant, then the strong expansion of grasses was peculiar. In the years following the treatments reinvasion of dicots was inhibited and strongly reduced. Regeneration was very slow. By the end of the 5th year following the spraying the number of dicot species was still less than half the number of dicot species before the treatment. The monocots had a share in the total percentage cover with 85-95% after 5 years. This value was 200-300% higher than in the intact community indicating complete disintegration of cover-abundance relations.

Table 2
Chemical treatments

Common name	Chemical name	Dose applied	Dates of treatments	Dates of recordings ⁺	Dates of soil-samplings	Type of action of herbicides
Gabonil	MCPA+dicamba	4 l/ha	June 1979	1979-1984 (5 years)		Selective leaf-herbicide of antiauxin type
	4-chloro-2-methyl phenoxy-acetic acid+2-methoxy-3,6-dichlorobenzoic acid	7 l/ha	June 1979 June 1980	1979-1984 (5 years)	1979-1984 (5 years) October	It expels the indolacetic acid from the biochemical processes
						It induces irregular cell-division, abnormalities in growth, metabolic troubles
Dalapon	2,2-dichloropropionic acid	12 kg/ha	June 1979	1979-1984 (5 years)		Selective leaf-herbicide of auxin type
		20 kg/ha	June 1979 June 1980	1979-1984 (5 years)	1979-1984 (5 years) October	It plays a role in utilization of the energy, it exerts an influence on the lipid metabolism
						Furthermore, it affects nitrogen metabolism, facilitates the degradation of protein to amino acids and increases the level of amids
						It inhibits the synthesis of panthothenate stimulating the growth

Table 2 (cont.)

Common name	Chemical name	Dose applied	Dates of treatments	Dates of recordings ⁺	Dates of soil-damplings	Type of action of herbicides
Glialka	glyphosate	15 l/ha	June 1980	1980-1984 (4 years)	1980-1984 (4 years) October	Leaf-herbicide having an effect on Monocots and Dicots
	N-/phosphono-methyl/glycine					It inhibits the aromatic amino-acid synthesis
Soil sterilization			January 1980	1980-1985 (4.5 year from Sept. 1980 to October 1984)	1980-1985 (4 years) October	

⁺Recordings were made twice a year, in June and in September

Dalapon 20 experiment

The dominant monocots were removed. Predominance of dicots was remarkable throughout the 5 years studied. It was very important that after eliminating the dominant species large bare ground occurred where some dicots well spreading by vegetative propagula became predominant and determined subsequent vegetation changes. The monocots re-appeared only 3-4 years later.

The changes in species number and percentage cover were very rapid. The sociological state characterized by the dominance of dicots proved to be unstable and very sensitive to stress (drought).

Glyphosate experiment

Glyphosate killed the vegetation completely, including the above-ground and the underground plant parts, but did not affect the seeds in the soil. The bare ground was recolonized initially from seeds, therefore this process can be considered a relatively typical secondary succession of an old grassland community. In the area after the treatment, the first species occupying the site were mainly dicots, but a few monocots also sprouted. The dominance of dicots was obvious throughout the whole period investigated.

Experiment on sterilized soil

This is an experimental study of primary succession (see VIRÁGH 1982 for details). It reflects well a certain replacement series of species groups. First a large number of annual "pioneer" species, such as Erigeron canadensis and Rumex acetosella, which grow rapidly and produce seeds in large quantities but have a low competitive ability, were observed. Then biennial species appeared, which were succeeded by perennials. Of the monocots, Agrostis canina and Anthoxanthum odoratum were the first species that occurred in the quadrats in the second and the third year of primary succession, and Festuca rupicola was the final occupant.

Experimental design

The area of $40 \times 30 \text{ m}^2$ marked out for the experimental purpose was enclosed in 1979, and it has not been used as a pasture since that time. The experiment was arranged in a randomized block design with five replications per treatment (40 plots in total). The treated quadrats are of $1.5 \times 1.5 \text{ m}^2$. The detailed investigations were carried out in permanent quadrats of $1 \times 1 \text{ m}^2$ size by means of an iron frame covered with a grid of 20×20 cm units (see VIRÁGH 1982).

The floristic composition was recorded twice a year, in June and September. Percentage cover of species was estimated in the contagious subquadrats (125 subquadrats in total per treatment). Sprayings were carried out at the end of June, 1979. In case of the selective herbicides of larger dose the treatments were repeated again after a year.

Soil sampling

In order to examine the seed bank of the soil, in October of every year from 1979 to 1984 samples were taken from a soil depth of 8.5 cm with a soil sampler, of an area of 19.6 cm² from the untreated (control), sterilized quadrats and from those treated by herbicides.

The soil samples investigated in the case of different treatments were the following:

Control	1981	5 samples	(Samples originated from 5 different quadrats to indicate variability among the "replications" in a certain year.)
Gabonil 7	1981	1 sample	
Dalapon 20	1981	1 sample	
Glyphosate	1980	1 sample	
	1981	1 sample	
	1982	1 sample	
	1983	1 sample	(Samples collected from the same quadrat at the same time in successive years.)
Sterile	1980	1 sample	
	1981	1 sample	
	1982	1 sample	
	1983	1 sample	(Samples collected from the same quadrat in every year.)

It must be noted that while the application of permanent quadrats was inevitable for vegetation dynamic studies, this method involved serious limitations for determining seed banks. One soil sample could be taken only from each of the treated quadrats in every year in order to avoid the effects of disturbance and to make the long-term vegetation studies possible. Since soil samples were taken once a year only, the persistent seed banks were detected but the transient seed banks were not. Seeds existing only during the dry season made little or no contribution to the seed banks examined, generally they were not found in the wet autumn.

Considering soil microheterogeneity and the strong patchiness of vegetation, 5 replications are certainly insufficient for a precise estimation of seed bank size. Small samples may not include seeds of rare species. It is also expected that variation between samples for the dominant species will be great, since the distribution of species is clumped in local depressions, on the edge of tussocks, etc.

Because of sampling problems the measurements of seed bank composition are best regarded as results of "survey sampling". The data thus obtained are useful to compare different treatments and to illustrate major trends during secondary and primary succession but are incomplete for a precise description of the seed bank size. The information was used to make some hypotheses on the role of seed banks after herbicide treatments, and on regeneration and colonization processes in the study area.

The estimates were expressed in terms of seed number per 200 cm³ soil volume of each sample. (We did not attempt to refer the counts to 1 m² area!)

Methods for estimating viable seeds (seed bank) in soil samples

The collected soil samples were air-dried in the laboratory, then they were kept in a cool place until the samples were processed. In order to avoid the disadvantages of the seedling emergence-technique (MALONE 1967, ROBERTS 1981, van der VALK and DAVIS 1978, JENSEN 1969, FAY and OLSON 1978), MALONE's method (1967) was chosen for determining seed banks. It is a reliable and probably one of the most effective procedures for estimating seed counts in the soil.

The method of MALONE involves physical and chemical dispersion of the soil, chemical flotation and extraction of organic debris and determination of viable seeds. The procedure requires a solution of 10 g sodium hexametaphosphate, 5 g sodium bicarbonate and 25 g magnesium sulphate dissolved in 200 ml tap water for 100 g soil. The first two chemicals induce the breakdown of soil aggregates and ensure efficient extraction of debris by flotation, accomplished by magnesium sulphate (MALONE 1967).

Many other different liquids have also been used as flotation media. Some workers prefer organic liquids such as tetrachloromethane (HYDE and SUCKLING 1953, DECHKOV 1975) or perchloroethylene (JONES and EVANS 1977). However, the most favoured and the most widely used solutions are the solutions of mineral salts, since they are cheap and present little health hazard (ROBERTS 1981). Among those used in recent studies are potassium carbonate (HAYASHI and NUMATA 1971), sodium carbonate (HAYASHI 1975), zinc chloride (BENCZE 1963, FEKETE 1975, HUNYADI and PATHY 1976) and calcium chloride (BARBOUR and LANGE 1967, ROBERTS and RICKETTS 1979).

Owing to the textural features of the soil, MALONE's method proved to be the fastest and the most convenient procedure, as well as the harmless method for the seeds.

The steps of separating the seeds from soil are summarized as follows:

- Homogenization of a 100 g sample of air-dried soil: crumbling of the larger soil lumps. (The seeds remained intact or by chance their scarification occurred.)

- Dry-sieving by shaking apparatus through a 1.4; 0.6 and 0.14 mm mesh sieve onto a collecting pan. (A sieve with 0.14 mm openings was sufficient for retaining also the small seeds.)

- Washing of the muddy parts of the soil carefully through the sieves of different mesh by tap water.

- Then the collected material on the sieves was transferred quantitatively to a 1000 ml volumetric flask. The solution of sodium hexametaphosphate, sodium bicarbonate and magnesium sulphate was added to the flask and the flask was shaken vigorously. The level of the solution was brought up to the mouth of the flask and the flask was left undisturbed for 30 minutes. At the end of this time, the seeds had floated to the top of the flask.

- The upper part of the solution was filtered by suction through Watman No 1 filter paper in a Buchner funnel. The filter paper was removed from the funnel, then it was dried at 25–30 °C carefully.

The sieving-flotation separating technique was followed by the identification of seeds selected from the soil. The seeds were counted and identified in each sample separately under a binocular stereomicroscope. Identification of the seeds was accomplished using a comparative material from the *Pulsatillo-Festucetum rupicolae* community and the atlas by SCHERMANN (1966).

To estimate the viability of seeds the method proposed by ZELENCHUK (1961) was chosen (see also HAYASHI et al. 1978, ROBERTS and RICKETTS 1979).

Those seeds were recorded only which appeared to be intact and which resisted gentle pressure. This is an accepted and reliable method of identifying "apparently viable" seeds; its great advantage is its rapidity and convenience if compared e.g., to the tetrazolium test (COLBRY et al. 1961, MALONE 1967).

RESULTS AND DISCUSSION

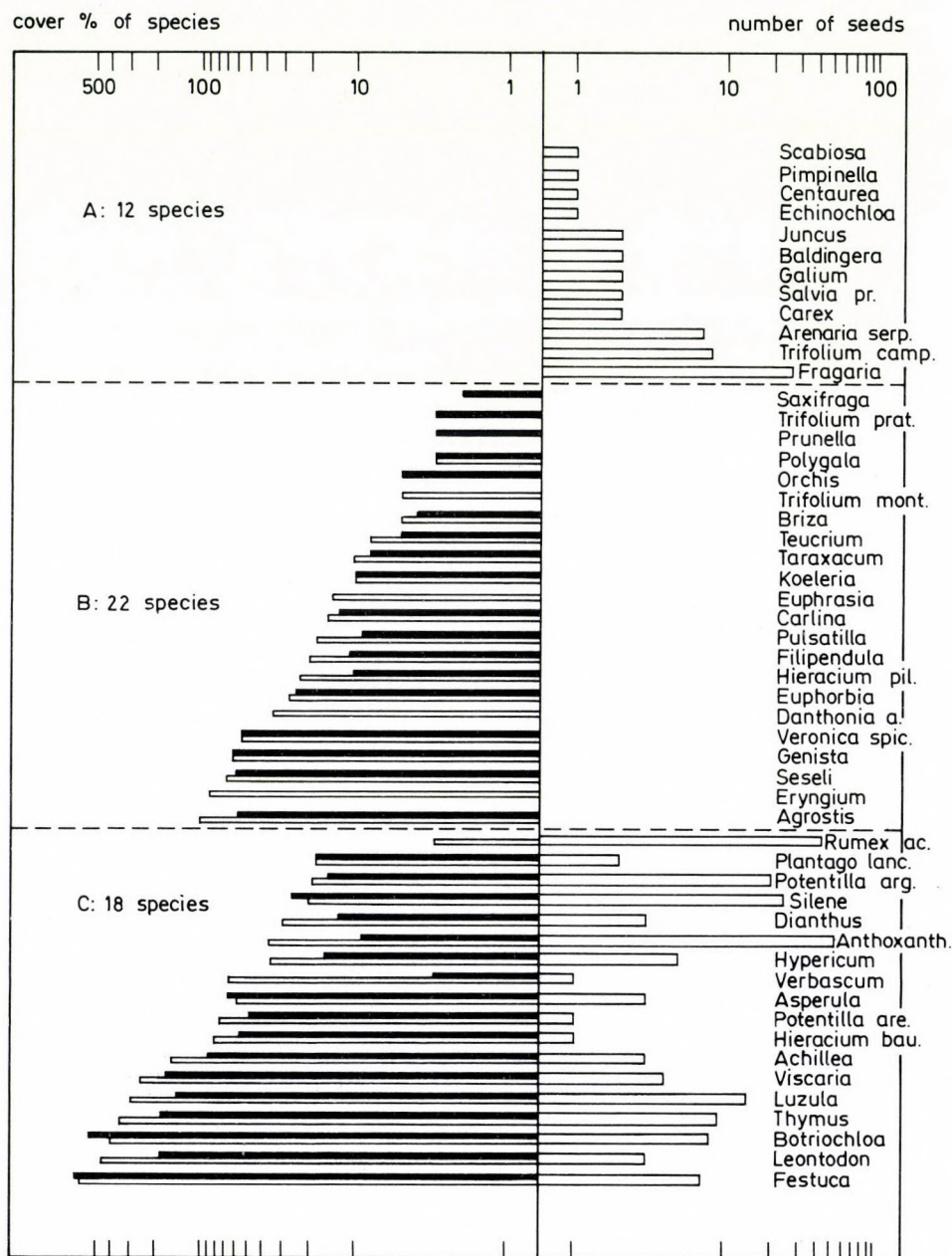
Results of seed banks study are presented in connection with the species composition of the associated vegetation.

Control experiment

The results referring to the original, intact community are demonstrated in Fig. 1 indicating the component species in the seed bank of the soil and in the aboveground flora, as well as the species present only in the seed bank and only in the aboveground vegetation in separated "groups".

It can be stated that the species composition in the seed bank is less diverse than the vegetation from which it was derived. The quadrats investigated in 1981 contained about 40 species in the summer and autumn growing period, and 75 percent of the species number can be found in the soil. This data can be regarded as a relatively high value, especially if we consider that the community consists of many rare species and due to the close and dense plant cover stand the seeds cannot get into the soil easily and the majority of the species present in the soil surface germinate rapidly.

It is remarkable that the most frequent and abundant species in the vegetation are represented by many seeds (18) in the persistent seed bank. Among the dominant species of the aboveground flora, Bothriochloa ischaemum, Thymus marshallianus and Luzula campestris species are also dominant as seeds in the soil. There are 22 component species of the vegetation which are completely absent from the seed bank in the given year, while there are 9 species present in the seed bank out of which 6 appear in the vegetation only 2 years later. There are 3 species (Galium verum, Pimpinella saxifraga, Salvia pratensis), which cannot surely germinate even in the subsequent some years studied. Seeds of two arable weeds originated from the environs, such as Baldingera and Echinochloa species are also present. A Juncus species come from a marsh found in the valley not far from the investigated



area is also represented as seeds. These species contribute to the seed bank of the grassland, but no seedlings of them were recorded during the six years of study. The seeds cannot germinate presumably because of the dense plant cover stand and the competition among the species. It must be noted that the dormancy of these species is guaranteed by their large hard-coated seeds, too.

In general, most of the species are represented by few (1-3) seeds in the soil. Scarcity of seeds may be related to the low reproductive vigor of the given populations and the large number of species spreading mainly by vegetative propagula. Conversely, there are some species rare in the vegetation, which are the major constituents of the seed bank with numerous seeds. These are, e.g., Rumex acetosella (43 seeds), Fragaria viridis (26), Silene otites (24) and Potentilla argentea (20).

Of the dominant grasses the seeds of Agrostis canina were entirely absent and relatively few seeds of Festuca rupicola, Bothriochloa ischaemum and Anthoxanthum odoratum species were recorded only. As it is well known, the seeds of most grasses are the major components of transient seed banks showing a strong peak in abundance of seeds in summer, so the representation of grasses as seeds even if with low number is of a great importance in the seed bank in October.

The seed bank in the untreated control quadrats was examined in 5 "replications" to get information on the variability among the samples (Table 3).

The standard deviations and coefficients of variation for the total number of seeds and for the total number of species illustrated in Table 3 indicate a great variation in seed number among the samples and a relatively small variation in the species number. If we neglect the samples with the largest and the smallest species number and seed number, CV% is reduced by more than half at about similar mean number of species and seeds (see Table 3). It seems likely that 10-15 replications are needed to provide

Fig. 1. Percentage cover of species and seed content of the soil in the control experiment, 1981. — A: number of species present only in the seed bank; — B: number of species present only in the established vegetation; — C: number of species present both in the vegetation and in the seed bank

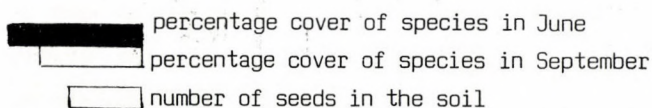


Table 3

Mean value of seed content in the control quadrats, its standard deviation and coefficient of variation

species (i)	samples (j)					$\sum_{j=1}^5 x_{ij}$	\bar{x}_i
	1	2	3	4	5		
1 <i>Agropyron repens</i>	-	-	5	-	-	5	$\bar{x}_1 = 1.0 \pm 1.0$ $Sx_1 = 2.23$
2 <i>Anthoxanthum odoratum</i>	35	9	28	6	53	131	$\bar{x}_2 = 26.2 \pm 8.67$ $Sx_2 = 19.38$
3 <i>Baldingera arundinacea</i> ⁺	-	-	-	-	2	2	$\bar{x}_3 = 0.4 \pm 0.4$ $Sx_3 = 0.89$
4 <i>Bothriochloa ischaemum</i>	2	5	12	3	8	30	$\bar{x}_4 = 6.0 \pm 1.81$ $Sx_4 = 4.06$
5 <i>Danthonia decumbens</i>	3	2	2	1	-	8	$\bar{x}_5 = 1.6 \pm 0.50$ $Sx_5 = 1.14$
6 <i>Echinochloa crus-galli</i> ⁺	7	-	-	-	1	8	$\bar{x}_6 = 1.6 \pm 1.36$ $Sx_6 = 3.04$
7 <i>Festuca rupicola</i> + <i>pseudovina</i>	2	6	40	3	7	58	$\bar{x}_7 = 11.6 \pm 7.15$ $Sx_7 = 16.00$
8 <i>Koeleria cristata</i>	-	-	16	-	-	16	$\bar{x}_8 = 3.2 \pm 3.2$ $Sx_8 = 7.15$
9 <i>Carex caryophyllea</i>	19	-	4	-	2	25	$\bar{x}_9 = 5.0 \pm 3.57$ $Sx_9 = 8.0$
10 <i>Juncus sp.</i> ⁺	-	-	-	-	2	2	$\bar{x}_{10} = 0.4 \pm 0.4$ $Sx_{10} = 0.89$
11 <i>Luzula campestris</i>	-	1	2	1	14	18	$\bar{x}_{11} = 3.6 \pm 2.61$ $Sx_{11} = 5.85$
12 <i>Achillea collina</i>	-	-	-	1	3	4	$\bar{x}_{12} = 0.8 \pm 0.58$ $Sx_{12} = 1.30$
13 <i>Arenaria serpyllifolia</i>	-	6	9	-	7	22	$\bar{x}_{13} = 4.4 \pm 1.86$ $Sx_{13} = 4.15$
14 <i>Asperula cynanchica</i>	7	-	-	-	3	10	$\bar{x}_{14} = 2.0 \pm 1.37$ $Sx_{14} = 3.08$
15 <i>Centaurea pannonica</i>	-	-	-	-	1	1	$\bar{x}_{15} = 0.2 \pm 0.2$ $Sx_{15} = 0.44$
16 <i>Chenopodium album</i>	-	-	2	-	-	2	$\bar{x}_{16} = 0.4 \pm 0.4$ $Sx_{16} = 0.89$
17 <i>Convolvulus arvensis</i>	2	-	-	5	-	2	$\bar{x}_{17} = 1.4 \pm 0.97$ $Sx_{17} = 2.19$
18 <i>Crataegus monogyna</i>	-	-	1	-	-	1	$\bar{x}_{18} = 0.2 \pm 0.2$ $Sx_{18} = 0.44$
19 <i>Dianthus pontederæ</i>	-	4	5	-	3	12	$\bar{x}_{19} = 2.4 \pm 1.2$ $Sx_{19} = 2.30$
20 <i>Echium vulgare</i>	1	-	-	1	-	2	$\bar{x}_{20} = 0.4 \pm 0.24$ $Sx_{20} = 0.54$
21 <i>Euphorbia cyparissias</i>	1	1	2	-	-	4	$\bar{x}_{21} = 0.8 \pm 0.37$ $Sx_{21} = 0.83$
22 <i>Fragaria viridis</i>	-	9	5	-	26	40	$\bar{x}_{22} = 8.0 \pm 0.48$ $Sx_{22} = 10.74$
23 <i>Galium verum</i>	-	2	-	-	2	4	$\bar{x}_{23} = 0.8 \pm 0.48$ $Sx_{23} = 1.09$
24 <i>Hieracium bauhinii</i>	-	1	-	-	1	2	$\bar{x}_{24} = 0.4 \pm 0.24$ $Sx_{24} = 0.54$
25 <i>Hypericum perforatum</i>	-	3	-	-	5	8	$\bar{x}_{25} = 1.6 \pm 1.02$ $Sx_{25} = 2.30$
26 <i>Leontodon hispidus</i>	2	5	4	3	3	17	$\bar{x}_{26} = 3.4 \pm 0.50$ $Sx_{26} = 1.14$
27 <i>Linum catharticum</i>	-	-	1	-	-	1	$\bar{x}_{27} = 0.2 \pm 0.2$ $Sx_{27} = 0.44$
28 <i>Pimpinella saxifraga</i>	1	-	-	1	1	3	$\bar{x}_{28} = 0.6 \pm 0.24$ $Sx_{28} = 0.54$
29 <i>Plantago lanceolata</i>	3	2	2	1	2	10	$\bar{x}_{29} = 2.0 \pm 0.31$ $Sx_{29} = 0.70$
30 <i>Potentilla arenaria</i>	-	-	-	-	1	1	$\bar{x}_{30} = 0.2 \pm 0.2$ $Sx_{30} = 0.44$

Table 3 (cont.)

samples (j)	1	2	3	4	5	$\sum_{j=1}^5 x_{ij}$	$\bar{x}_{i.}$
species (i)							
31 <i>Potentilla argentea</i>	15	19	20	17	20	91	$\bar{x}_{31}=18.2^{+0.96}$ $Sx_{31}=2.16$
32 <i>Prunella laciniata</i>	-	-	-	4	-	4	$\bar{x}_{32}=0.8^{+0.8}$ $Sx_{32}=1.78$
33 <i>Rumex acetosella</i>	6	29	10	11	43	99	$\bar{x}_{33}=19.8^{+7.02}$ $Sx_{33}=15.70$
34 <i>Salvia pratensis</i>	2	9	6	3	2	22	$\bar{x}_{34}=4.4^{+1.36}$ $Sx_{34}=3.04$
35 <i>Scabiosa ochroleuca</i>	1	5	-	-	1	7	$\bar{x}_{35}=1.4^{+0.99}$ $Sx_{35}=2.07$
36 <i>Silene otites</i>	-	5	4	-	17	26	$\bar{x}_{36}=5.2^{+3.12}$ $Sx_{36}=6.97$
37 <i>Silene pseudotites</i>	4	-	-	-	7	11	$\bar{x}_{37}=2.2^{+1.42}$ $Sx_{37}=3.19$
38 <i>Thymus marschallianus</i>	-	-	-	-	9	9	$\bar{x}_{38}=1.8^{+1.8}$ $Sx_{38}=4.02$
39 <i>Trifolium campestre</i>	7	7	1	1	8	24	$\bar{x}_{39}=4.8^{+1.56}$ $Sx_{39}=3.49$
40 <i>Verbascum phoeniceum</i>	-	9	-	-	1	10	$\bar{x}_{40}=2.0^{+1.76}$ $Sx_{40}=3.93$
41 <i>Vicia cassubica</i>	-	-	2	-	-	2	$\bar{x}_{41}=0.4^{+0.4}$ $Sx_{41}=0.89$
42 <i>Viscaria vulgaris</i>	5	-	3	2	4	14	$\bar{x}_{42}=2.8^{+0.86}$ $Sx_{42}=1.92$
total number of seeds $y_j = \sum_{i=1}^{42} y_j \quad (j=1, \dots, 5)$	125	139	186	64	271	785	$\bar{y}_j = 157^{+34.52}$ $CV\%_{\bar{y}_j} = 49.2$
total number of species $y_j = \sum_{i=1}^{42} y_j \quad (j=1, \dots, 3)$	20	21	24	17	31		$\bar{y}_j = 22.6^{+2.37}$ $CV\%_{\bar{y}_j} = 23.5$
total number of seeds $x_j = \sum_{i=1}^{42} x_j \quad (j=1, \dots, 3)$	125	139	186			450	$\bar{x}_j = 150^{+18.44}$ $CV\%_{\bar{x}_j} = 21.3$
total number of species $y_j = \sum_{i=1}^{42} y_j \quad (j=1, \dots, 3)$	20	21	24				$\bar{y}_j = 21.66^{+1.2}$ $CV\%_{\bar{y}_j} = 9.6$

statistically sufficient data on the qualitative and quantitative aspects of the seed bank. It must be emphasized that for a given species taken separately a high variability of seed number exists between the samples (see Table 3), so much more samples are needed for estimating the density of seeds of a given species.

Gabonil 7 experiment

The composition of seed bank in the quadrat treated by Gabonil does not reflect the floristic composition of the present vegetation 2 years after spraying (Fig. 2). It is, however, much more similar to the species composition of the seed bank in control quadrats and less similar to the above-ground floristic composition in the "Gabonil quadrat" before spraying. Similarities in the abundance relations between the seed banks of control and Gabonil quadrats are demonstrated in Table 4. It appears that eight species out of the 10 most abundant species in the soil are the same in both experiments.

Table 4

The ten most dominant species in the seed bank of the control and Gabonil quadrats

order \ treatment	Control		Gabonil 7	
	species	number of seeds	species	number of seeds
1	<u>Anthoxanthum</u> ⁺	53	<u>Rumex acetosella</u> ⁺	87
2	<u>Rumex acetosella</u> ⁺	43	<u>Anthoxanthum</u> ⁺	43
3	<u>Fragaria</u> ⁺	26	<u>Arenaria serp.</u> ⁺	19
4	<u>Silene</u>	24	<u>Trifolium camp.</u>	18
5	<u>Potentilla argentea</u> ⁺	20	<u>Carex</u>	16
6	<u>Luzula</u>	14	<u>Potentilla arg.</u> ⁺	16
7	<u>Thymus</u> ⁺	8	<u>Festuca</u> ⁺	12
8	<u>Bothriochloa</u> ⁺	8	<u>Bothriochloa</u> ⁺	8
9	<u>Arenaria serp.</u> ⁺	7	<u>Thymus</u> ⁺	7
10	<u>Festuca</u> ⁺	7	<u>Fragaria</u> ⁺	6

⁺Species dominant in both experiments

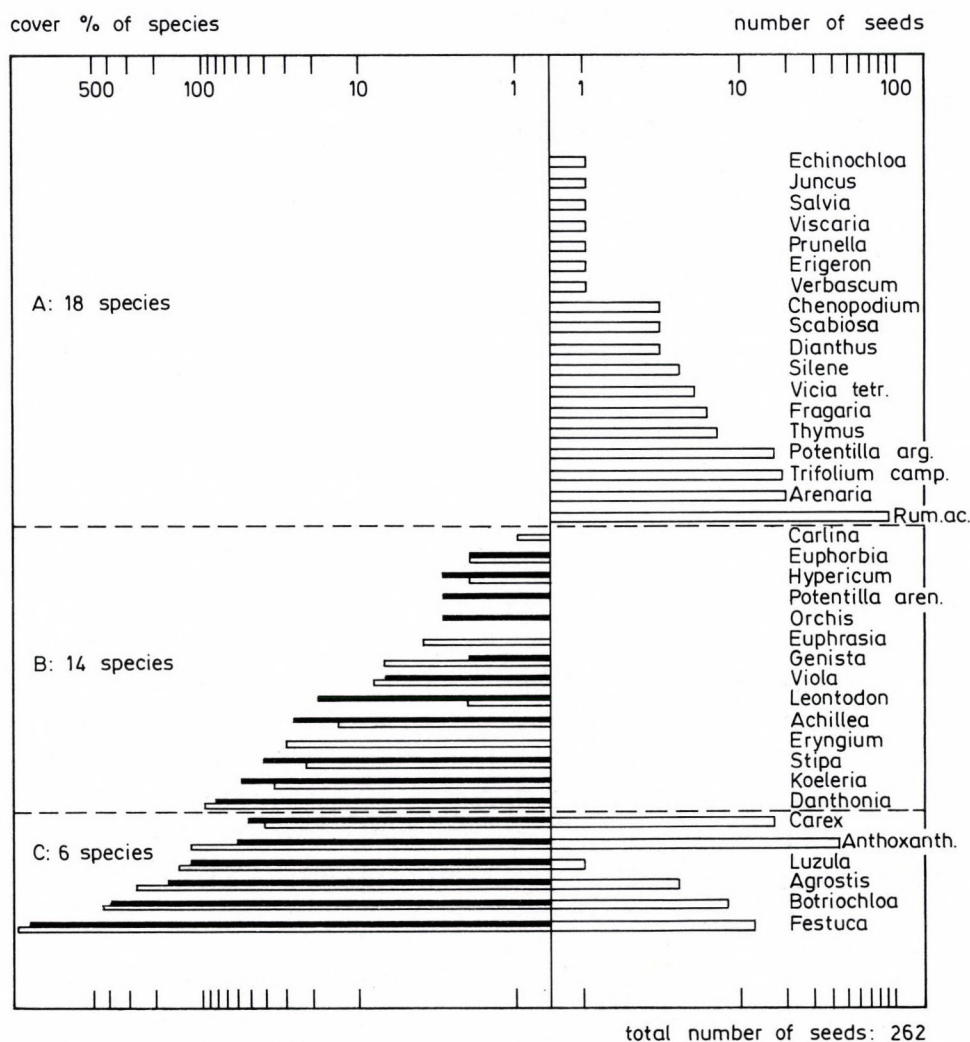


Fig. 2. Percentage cover of species and seed content of the soil in the Gabonil 7 experiment, 1981 (see Fig. 1. for explanation of symbols)

The results illustrated in Fig. 2 stress the importance of the presence of many dicotyledonous species in the soil with numerous seeds. Since it has been known that most of the dicots are absent from the above-ground flora and the others are infrequent with low percentage cover 3 years later after the treatments, it appears to be a very slow regeneration in this experiment. Though the seed bank provides a potential possibility for dicots to establish, the germination of their seeds is probably

inhibited partly due to the strong expansion of monocots occupying the bare ground. Vegetative way of regeneration is likely to be supported by the presence of nine dicots whose seeds are completely absent from the soil. These latter species spreading well by vegetative propagula can invade into the quadrats, but there they cannot reach their reproductive stage.

The number of monocots and the quantity of their seeds in the seed bank are similar to those in the control quadrats (cf. Table 3). Although the percentage cover of grasses became almost threetimes higher by 1981 than before the spraying, no increase of the seed content in the soil could be detected.

Dalapon 20 experiment

In this experiment, where monocots were killed and eliminated from the community, one of the most striking features of the results is that the seed bank does not contain graminoid seeds, with the exception of Anthoxanthum odoratum (Fig. 3).

Festuca rupicola and Agrostis canina species were predominant in the vegetation before the treatment, but they are entirely absent from the seed reservoir after spraying. It indicates that the grasses do not have long-lived seeds. The failure of the grasses to develop a persistent seed bank in the soil is already well-documented (BRECHLEY and WARINGTON 1930, CHIPPINDALE and MILTON 1934, MILTON 1939, CHAMPNESS and MORRIS 1948, THOMPSON and GRIME 1979) and supported also by our findings obtained from the control and Gabonil experiments. The seed of grasses contributed a little to the seed bank of the grassland, but probably due to the enormous fresh seed input the graminoid species were always represented in the soil at least with a few seeds in the intact and Gabonil-treated plots.

In the Dalapon quadrats there is no fresh grass seed input and none of the wind-dispersed seeds falling to the bare ground by chance has occurred in the soil. Anthoxanthum odoratum is the only monocot whose seeds were present in the seed bank in October. Its reason may be that this species, which has no green parts in June, in the time of spraying, could not be killed by the herbicide. Hence in this case the permanent seed input was not stopped and there were always some Anthoxanthum seeds which could not germinate immediately after their falling off and were able to appear in the seed bank.

The seed bank contain a high number of dicots. The total number of dicotyledonous species corresponds to that in the control soil-samples, but

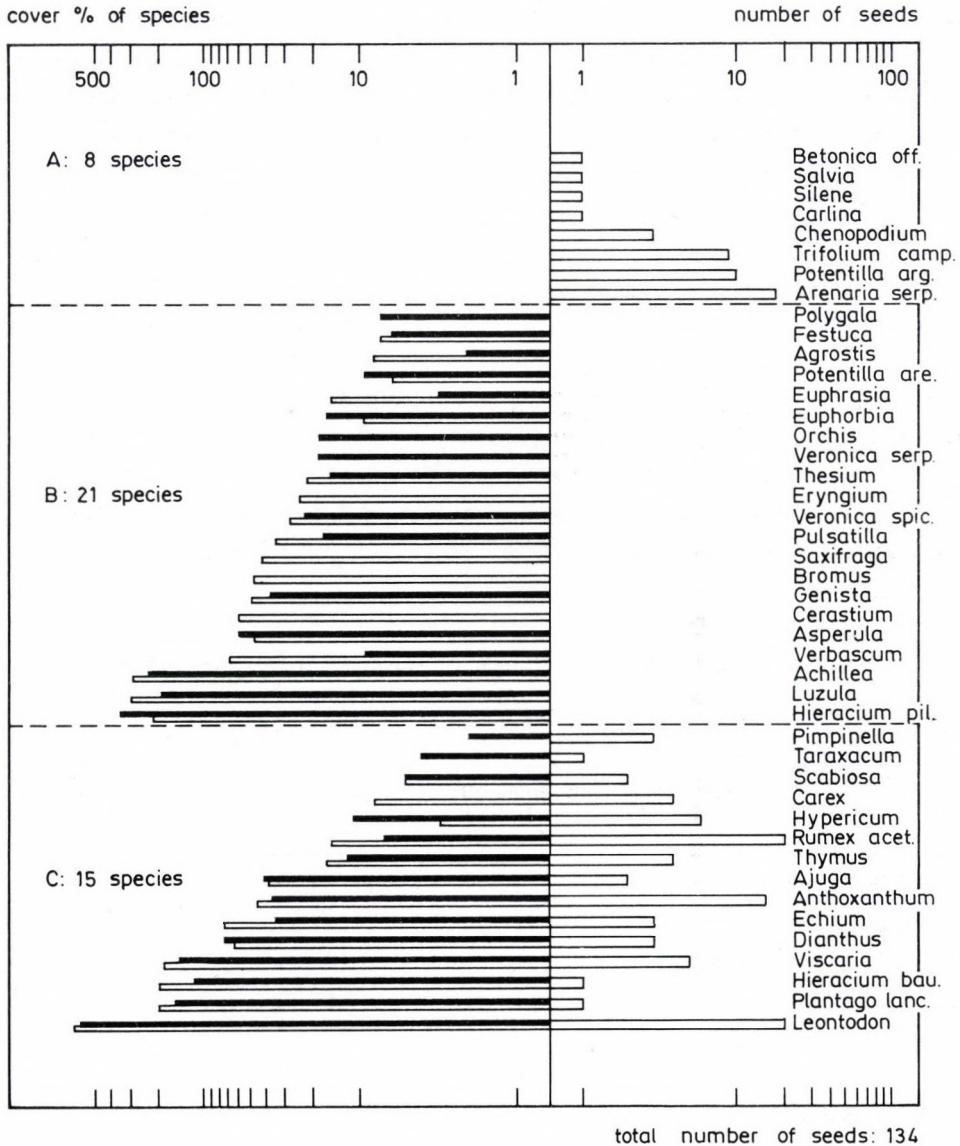


Fig. 3. Percentage cover of species and seed content of the soil in the Dalapon 20 experiment, 1981 (see Fig. 1. for explanation of symbols)

seed content is much less than in the intact original community, reflecting the influence of the treatment rather than the past vegetation. In this experiment rapid vegetative spreading of some dicots after the herbicide spraying was the most typical. Regenerative vigor of these species was very little. There were some dicots, dominant in the established vegetation, such as Hieracium pilosella, Hieracium bauginii, Achillea collina and Plantago lanceolata, whose seeds hardly could be found in the soil.

Comparison of the seed bank of the Dalapon quadrat with the Gabonil and control ones suggests that of the 10 most dominant species in the soil 6 species are common in every experiment (Table 5). These species are Rumex acetosella, Anthoxanthum odoratum, Thymus marshallianus, Arenaria serpyllifolia, Potentilla argentea and Trifolium campestre. Since the latter three species are dominant neither in the intact nor in the treated quadrats but their seeds always predominate in the soil, therefore we considered these species highly seed-accumulating ones.

Table 5

Dominant species in the seed bank of three different experiments

Species	Treatment	Number of seeds		
		Dalapon 20	Gabonil 7	Control
<u>Leontodon hispidus</u>		20	-	-
<u>Rumex acetosella</u>		20	87	43
<u>Arenaria serpyllifolia</u>		18	19	7
<u>Anthoxanthum odoratum</u>		15	43	53
<u>Potentilla argentea</u>		10	16	20
<u>Trifolium campestre</u>		9	18	8
<u>Hypericum perforatum</u>		6	-	-
<u>Viscaria vulgaris</u>		5	-	-
<u>Thymus marshallianus</u>		4	7	9
<u>Carex caryophylla</u>		4	16	-

Glyphosate experiment

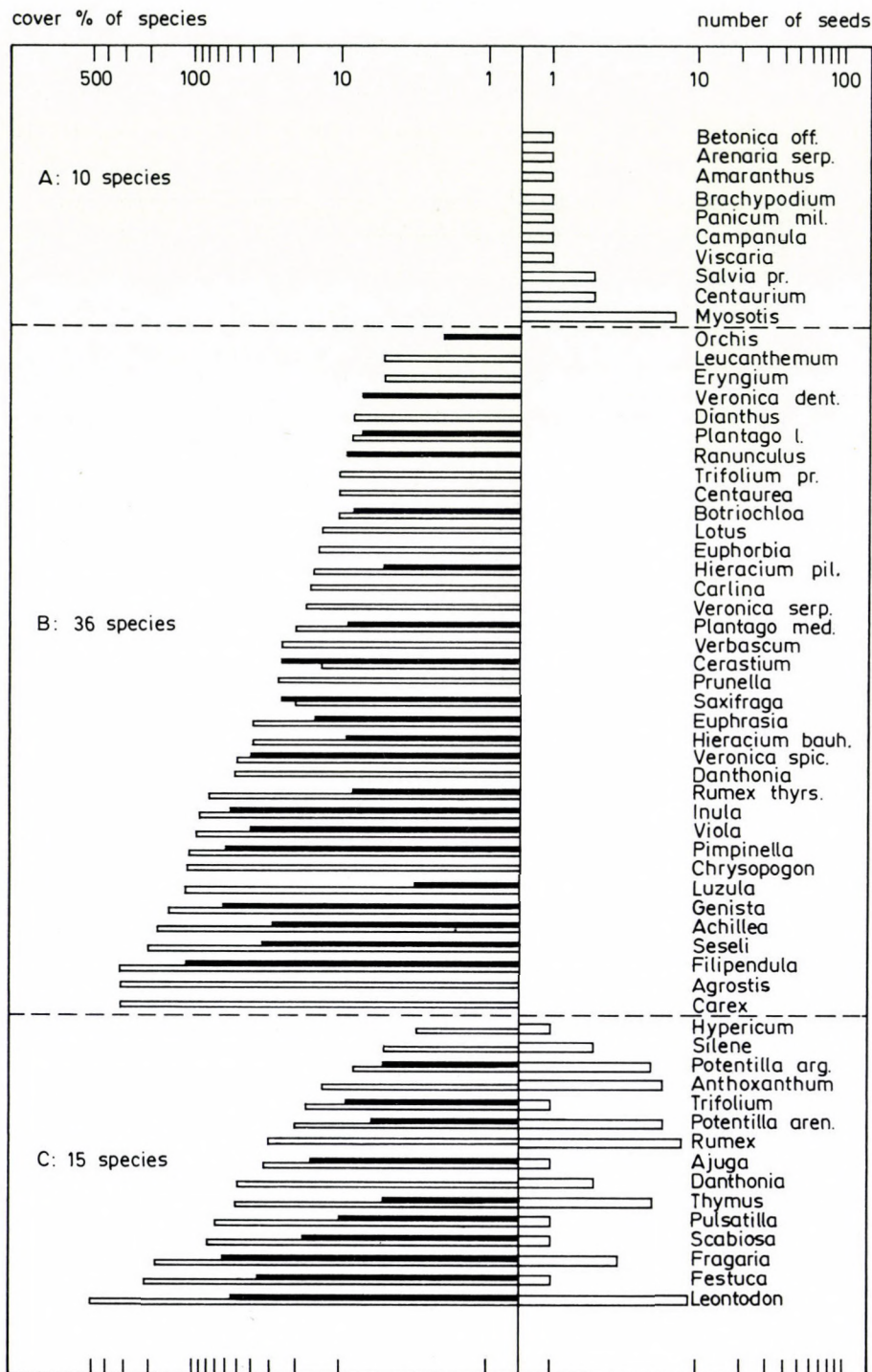
After having destroyed all the vegetation in June of 1980, colonization of the area immediately started in that autumn. Although it was noted above that the seed bank was relatively small in the grassland and its role in regeneration was insignificant, in the early phase of the secondary succession taking place in the Glyphosate quadrat we could suppose a great importance of the seed bank establishing an initial floristic composition in the bare ground. Fifteen species are common in the established vegetation and in the seed bank of the soil. Germination requirements of very few of the seeds present in the seed bank (e.g.: Arenaria serpyllifolia, Salvia pratensis, Viscaria vulgaris) were not met in the early phase of succession. There are, however, many species (33-36) present only in the vegetation but absent from the seed bank (Fig. 5). Moreover, the aboveground dominance of eight species (Filipendula vulgaris, Achillea collina, Genista tinctoria, Inula britannica, Pimpinella saxifraga, Veronica spicata, Viola arenaria, Seseli annuum) is considerable, but their seeds are not represented at all in the soil. This observation appears to support the conclusion that colonization of the given area went on not only from the seeds but by the invasion of vegetatively propagating species into the quadrats.

The total number of species in the seed bank shows little changes, but the composition has altered during the period investigated (Figs 4-7, Table 6). Only three or four species (Leontodon hispidus, Anthoxanthum odoratum and Festuca rupicola) were similarly dominant in the 4 years studied.

The number of seeds is the lowest in 1980. At that time due to the complete removal of the existing vegetation from the quadrat the influx of fresh seeds was prevented and many species developed by the autumn were not able to reach their reproductive stage. The highest seed content of the seed bank was estimated in the second year of the succession, which showed a declining tendency during the successive years.

Sterile experiment (Experiment on sterilized soil)

This study emphasizes the potential importance of seed bank during primary succession. It is notable in the early phase of succession that the number of species in the seed bank is much higher than that of in the established vegetation. It seems reasonable to expect that possession of a species rich and relatively large seed bank may allow many species to exist



or to become abundant later in the aboveground flora. There were relatively few species whose seeds were represented in the soil but they could not germinate and develop in the vegetation during the 4 years of observation. These species, in which the seeds remain dormant or viable for only a short time, are the following: Bothriochloa ischaemum, Carex caryophyllea, Danthonia decumbens, Danthonia alpina, Trifolium campestre, Asperula cynanchica, Filipendula vulgaris, Verbascum phoeniceum, and some forest-steppe species occurring only in the vicinity of the studied area, such as Thalictrum minus, Peucedanum oreoselinum, and such as Ononis spinosa, Chenopodium album and Echinochloa crus-galli originating from the cultivated area near the grassland sampled.

The number of the species found only in the vegetation but not in the seed bank is the lowest among all the experiments. Sixteen to eighteen species are present only in the aboveground flora in each year, but their seeds, with the exception of 3-5 species, were extracted from the soil during the 4 years of primary succession.

In the course of succession, the species number of the seed bank increases gradually. By contrast, the seed content shows a continuous decrease after its early strong increases (Table 7). The quantity of seeds is very small at the very beginning of the succession, but just one year later it already reaches its maximum, which is followed by a rapid increase. The data obtained in this experiment indicate that first of all the behaviour of Rumex acetosella may be responsible for these changes. This is the species that can be considered as the most significant contributor to the seed bank. It produces exceedingly large number of seeds in the first years of succession, and later, because of its low competitive capability, it becomes suppressed by other component species of the vegetation.

It is worth mentioning that this species being average frequent or rare element of the original intact grassland community, behaves as a pioneer one during the early stage of primary succession, but has also a persistent seed bank. The percentage cover in the aboveground vegetation and the seed content in the soil of Rumex acetosella are demonstrated below:

Fig. 4. Percentage cover of species and seed content of the soil in the Glyphosate experiment, 1980 (see Fig. 1. for explanation of symbols)

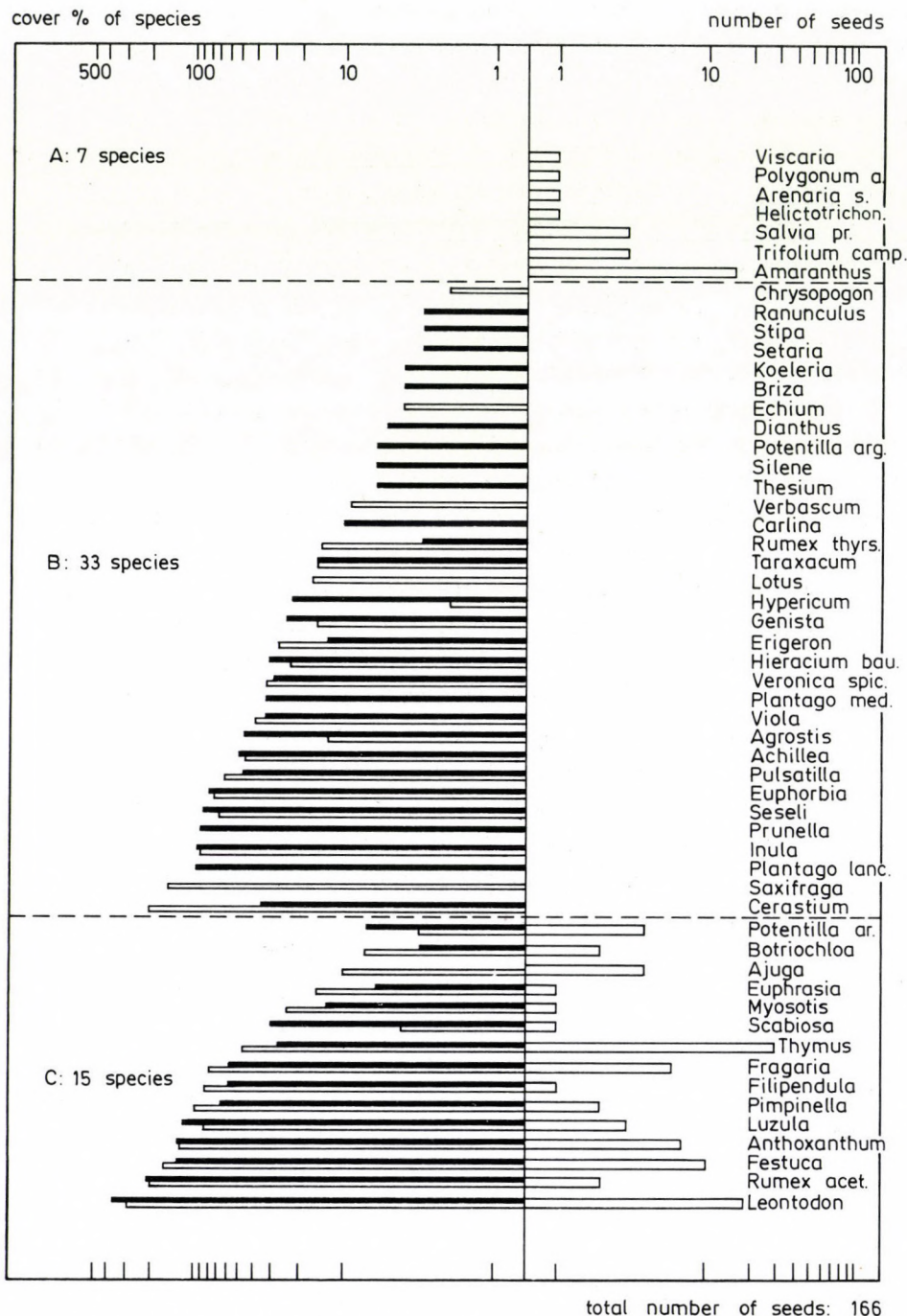


Fig. 5. Percentage cover of species and seed content of the soil in the Glyphosate experiment, 1981 (see Fig. 1. for explanation of symbols)

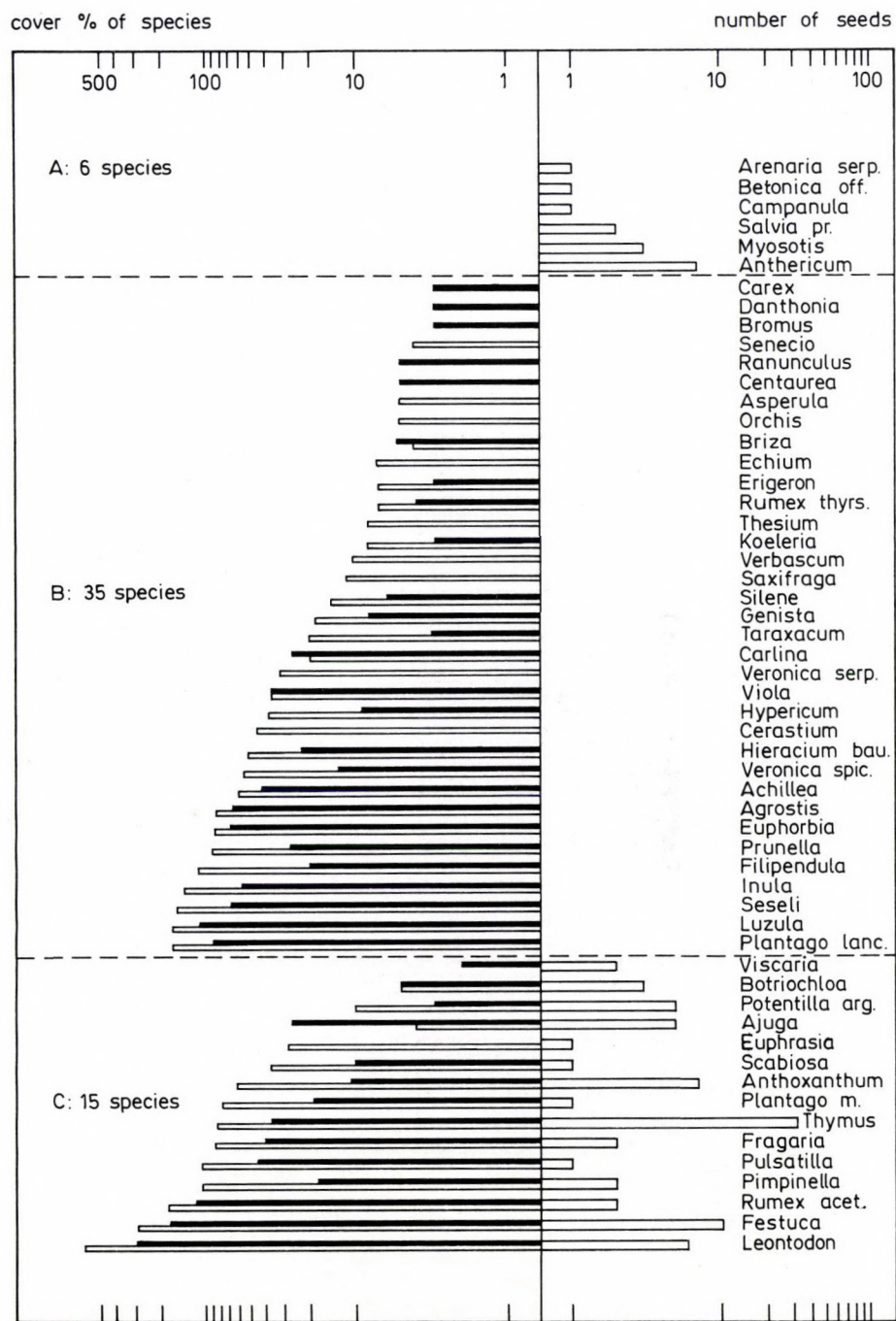


Fig. 6. Percentage cover of species and seed content of the soil in the Glyphosate experiment, 1982 (see Fig. 1. for explanation of symbols)

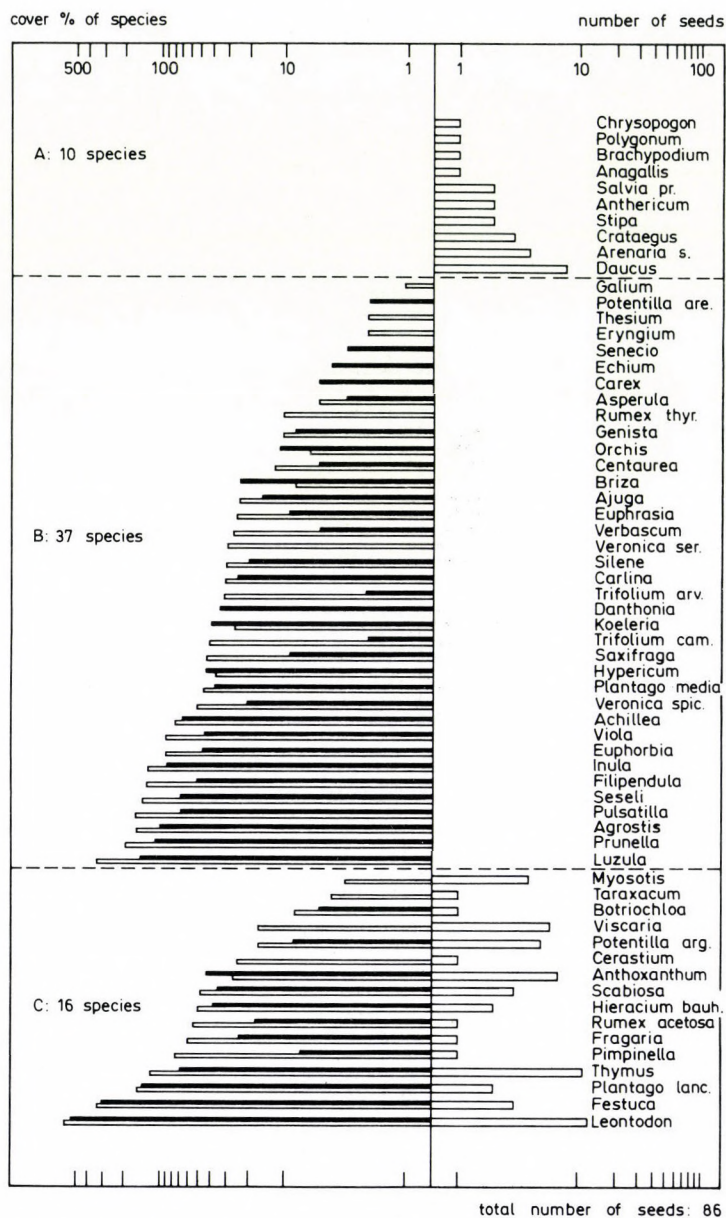


Fig. 7. Percentage cover of species and seed content of the soil in the Glyphosate experiment, 1983 (see Fig. 1. for explanation of symbols)

Table 6

Temporal changes of number of seeds and species number in the soil during the secondary succession in the Glyphosate experiment

A: Temporal changes in number of seeds of the first 10–11 most abundant species; B: Changes in total number of species and seeds

rank order of species	date of sampling	1980		1981		1982		1983	
		species	number of seeds	species	number of seeds	species	number of seeds	species	number of seeds
A	1	<u>Leontodon</u>	9	<u>Thymus</u>	29	<u>Thymus</u>	31	<u>Leontodon</u>	12
	2	Rumex a.	8	<u>Leontodon</u>	18	<u>Festuca</u>	10	<u>Thymus</u>	11
	3	Myosotis	7	Amaranthus	15	<u>Anthoxanthum</u>	7	Daucus	8
	4	Pot. are.	6	<u>Festuca</u>	10	Anthericum	7	<u>Anthoxanthum</u>	7
	5	<u>Anthoxanthum</u>	6	<u>Anthoxanthum</u>	7	<u>Leontodon</u>	6	Viscaria	6
	6	<u>Thymus</u>	5	Fragaria	6	Ajuga	5	Pot. arg.	5
	7	Pot. arg.	5	Ajuga	4	Pot. arg.	5	Myosotis	4
	8	Fragaria	3	Pot. aren.	4	Bothriochloa	3	Arenaria s.	4
	9	<u>Festuca</u>	1	Luzula	3	Myosotis	3	<u>Festuca</u>	3
	10			Trif. camp.	3			Scabiosa	3
	11			Salvia prat.	3				
B	total number of species	25		22		21		23	
	total number of seeds	70		130		97		72	

Underlining () indicates the species dominant in each of the four years

Table 7

Changes in abundance value of the component species of the vegetation (A) and of the seed bank (B) during the primary succession. a: name of species; b: percentage cover (%); c: number of seeds

rank order of species	date of sampling	1980		1981				1982			
		September		June		September		June		September	
		a	b	a	b	a	b	a	b	a	b
A	1	Rumex a.	285	Rumex a.	1087	Rumex a.	857	Rumex a.	619	Euphorbia	348
	2	Setaria	57	Euphorbia	213	Euphorbia	322	Euphorbia	460	Festuca	324
	3	Thymus	44	Achillea	42	Setaria	123	Festuca	200	Hier.bau.	157
	4			Thymus	56	Hier.bau.	119	Hier.bau.	197	Agrostis	99
	5			Festuca	29	Festuca	97	Thymus	123	Thymus	96
	6			Agrostis	5	Thymus	73	Achillea	58	Achillea	85
	7			Setaria	3	Achillea	64	Koeleria	75	Rumex a.	58
	8					Koeleria	25	Leontodon	74	Pot.are.	69
	9					Agrostis	10	Pot.are.	60	Leontodon	16
	10							Agrostis	53	Koeleria	32
	11							Anthoxanthum	42	Setaria	26
	12									Anthoxanthum	19
total number of species		12				24		26			
B		a	c			a	c	a			
	1	Euphrasia	13			Rumex a.	155			Rumex a.	46
	2	Setaria	8			Hypericum	30			Hypericum	27
	3	Pot.arg.	5			Convolvulus	27			Viscaria	18
	4	Viscaria	5			Viscaria	23			Setaria	11
	5	Asperula	4			Plant.lance.	12			Cerastium	9
	6	Trif.camp.	4			Trif.camp.	10			Silene	5
	7	Anthoxanthum	3			Pot.arg.	9			Chenopodium	5
	8	Rumex a.	2			Anthoxanthum	4			Galium	4
	9	Bothriochloa	1			Luzula	4			Trif.camp.	3
	10					Festuca	3				
total number of species		18				22		25			
total number of seeds		57				296		155			

Table 7 (cont.)

rank order of speices	date of sampling	1983				1984			
		June		September		June		September	
		a	b	a	b	a	b	a	b
A	1	Euphorbia	423	Koeleria	344	Koeleria	397	Festuca	364
	2	Festuca	308	Festuca	245	Festuca	324	Koeleria	146
	3	Hier.bau.	260	Hier.bau.	178	Hier.bau.	316	Thymus	120
	4	Koeleria	202	Euphorbia	175	Thymus	230	Hier.bau.	87
	5	Thymus	190	Thymus	114	Euphorbia	181	Achillea	73
	6	Achillea	69	Achillea	112	Achillea	123	Euphorbia	63
	7	Dianthus	57	Hypericum	29	Pot.are.	89	Dianthus	56
	8	Agrostis	38	Agrostis	22	Dianthus	83	Pot.are.	39
	9	Anthoxanthum	34						
total number of species		33				35			
		a		c					
B	1			Agrostis	25				
	2			Echinochloa	17				
	3			Pot. arg.	11				
	4			Carex	11				
	5			Thymus	7				
	6			Anthoxanthum	7				
	7			Hypericum	7				
	8			Hier.bau.	6				
	9			Pot.are.	6				
	10			Rumex a.	2				
	11			Festuca	2				
	12			Bothriochloa	2				
total number of species		29							
total number of seeds		134							

	1980 Sept.	1981 June Sept.	1982 June Sept.	1983 June Sept.	1984 June Sept.
percentage		1087	619	8	0
cover	285	857	58	5	0
number of seeds in the soil (in October)	2	155	46	2	

By comparing the changes in dominance relations in the aboveground flora and in the seed bank of the soil (Table 7) some findings related to the life strategies of the species can be also revealed. In general, re-

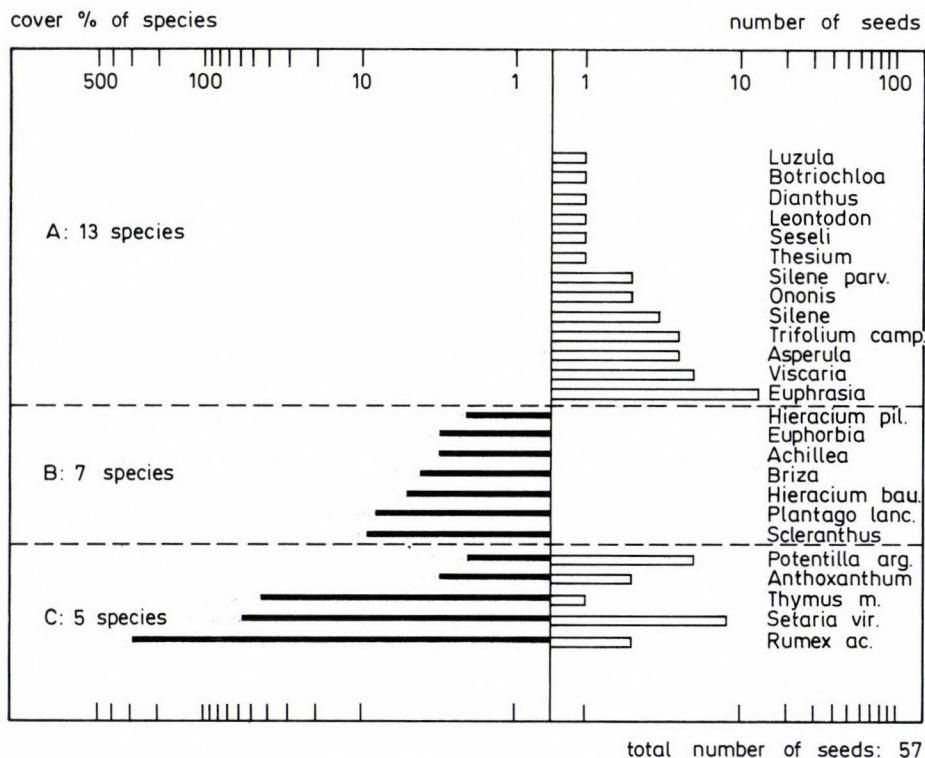


Fig. 8. Percentage cover of species and seed content of the soil in the experiment on sterilized soil, 1980 (see Fig. 1. for explanation of symbols)

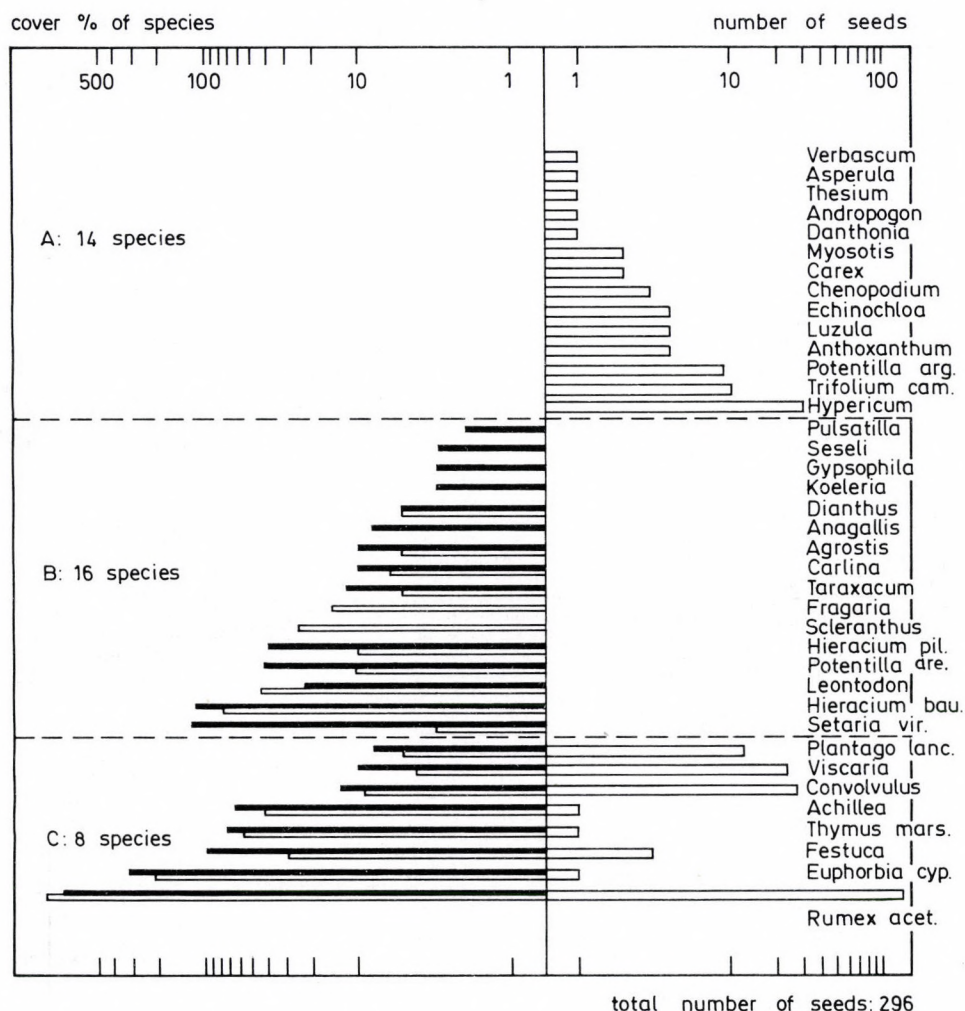


Fig. 9. Percentage cover of species and seed content of the soil in the experiment on sterilized soil, 1981 (see Fig. 1. for explanation of symbols)

placement of different species groups is well presented in the vegetation, but similar changes cannot be found in the composition of the seed bank except for 1-2 species. The seeds of Achillea collina and Euphorbia cyparissias species dominant already in 1981 in the vegetation are under-represented in the soil (cf. Figs 8-11). It indicates the main importance of vegetative expansion of these species and the possibility of their growing from seeds. In contrast to these two species, others, e.g., Thymus marschalianus, Hieracium bauginii and Hieracium pilosella, which are similarly

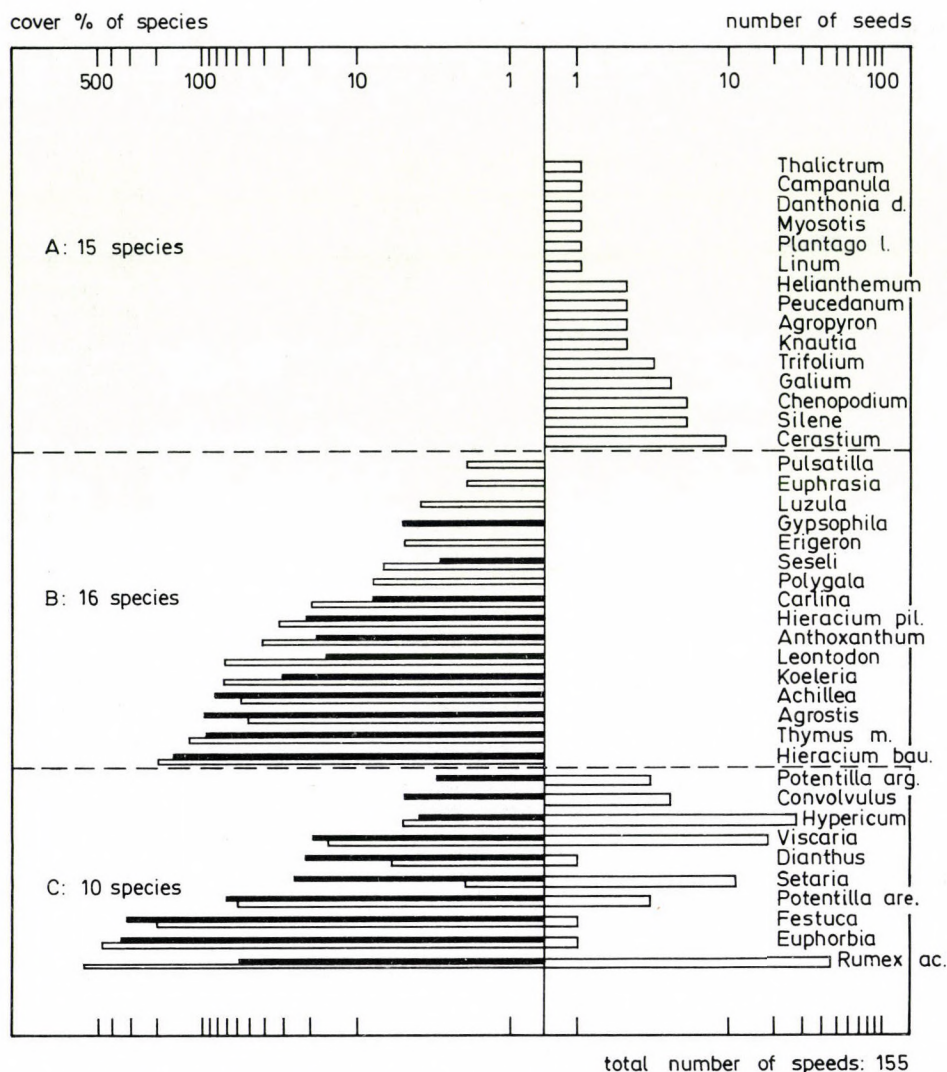


Fig. 10. Percentage cover of species and seed content of the soil in the experiment on sterilized soil, 1982 (see Fig. 1. for explanation of symbols)

dominant at the beginning of the succession, appear to exist only in vegetative phase for some years. The year of 1983 is the first when their seeds can be extracted from the soil. The behaviour of Koeleria cristata and Agrostis canina is similar to that of Thymus marschallianus and Hieracium pilosella. The seeds of Anthoxanthum odoratum are relatively well-represented, but the seeds of Festuca rupicola are very scarce in the soil, likewise in the experiments of other type.

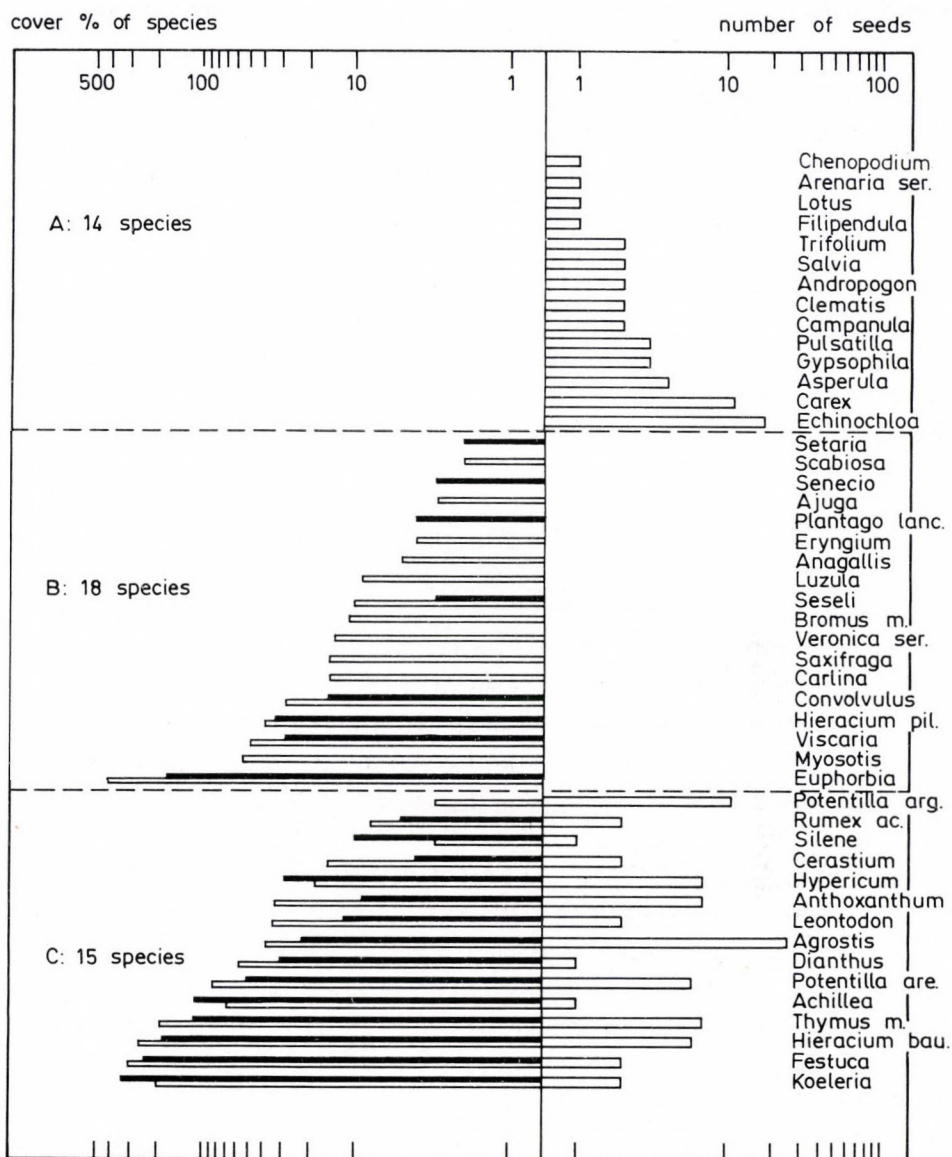


Fig. 11. Percentage cover of species and seed content of the soil in the experiment on sterilized soil, 1983 (see Fig. 1. for explanation of symbols)

Finally, comparison between Glyphosate and Sterile experiments shows that the early stage of secondary succession by the vegetative colonization, as well as by the species first germinating and occupying the bare ground after the treatment, whereas the primary succession taking place on sterilized soil is determined above all by the species growing rapidly and producing many seeds. The dominance of different species in the quadrats treated by Glyphosate mainly depends on the rate of colonization and for the later changes limitation of the bare ground and nutrient supply can be responsible. The bare ground on the sterilized soil remains favourable for the germination and colonization of many of the species for long years and major influence of different reproductive and survival capability of the species is a decisive importance.

Summary and some concluding remarks

The sampling used in this study provides an incomplete assessment of the size and composition of the seed banks, but gives useful information for interpreting the response of vegetation to disturbance and on the mechanism of vegetation dynamical processes taking place in the grassland community after the herbicide treatments. Seed bank data obtained were also used to formulate hypotheses about the role of the seed bank during successions of different type.

It was concluded that the role of seed banks in the regeneration and successional processes of the old semi-natural grassland community was insignificant. Regeneration by seeds appeared to play an important role only in the early stage of secondary succession and during primary succession. Recovery and colonization were achieved mainly through vegetatively propagating species, hence seed banks in this study could not be used in the prediction of species composition.

The results obtained for different experiments (treatments) documented the lack of close correspondence between the persistent seed bank and the aboveground vegetation. Seed banks reflected the past vegetation before spraying and the effects of herbicide treatments rather than the present vegetation. However, it must also be emphasized that disregarding, e.g., the dormancy of seeds and the very different germination requirements for the very reason that the measurement units (percentage cover of species and number of seeds in the soil) were not equivalent, the comparison of the

species composition of the seed bank with that of emerged adult plants cannot be completely justified. The shower of seeds onto the soil could give a more appropriate basis for assessment of similarity of the above- and below-ground populations in a certain year (see also RABINOWITZ 1981, RABINOWITZ and RAPP 1980). It would be especially obvious for our grassland community examined, where the viability of most seeds in the soil was short (short-lived seeds) and the role and the size of transient seed banks was not more important than the persistent seed banks.

The results of seed bank studies and their implications are relevant to the problem of vegetation dynamics both in theory and practice. However, it is also obvious, that these investigations must be continued together with additional population biological studies of life cycles, life strategies, seed production of species and seed dispersal. These joint investigations are very much needed to obtain more comprehensive results on the role of seed banks.

REFERENCES

- Barbour, M.G., Lange, R.T. (1967): Seed populations in some natural Australian topsoils. Ecology 48: 153-155.
- Barcsák, Z. (1968): Vegyszeres gyomirtás és műtrágyázás hatása a gyepek növényzetének összetételére és takarmány értékére. (The effect of chemical weed control and fertilization on floristic composition and on quality of forage of the pasture.) Manuscript, Gödöllő.
- Bartolome, J.W. (1979): Germination and seedling establishment in California annual grassland. J. Ecol. 67: 273-281.
- Belsky, A.J. (1986): Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. J. Ecol. 74: 419-437.
- Bencze, J. (1963): A szántóföldi gyomfertőzés prognózisa. (Prediction of weed-infection of arable fields.) Búvár 8: 195-199.
- Brenchley, W.E., Warrington, K. (1930): The weed seed population of arable soil. I. Numerical estimation of viable seeds observations on their natural dormancy. J. Ecol. 18: 235-272.
- Chamness, S.S., Morris, K. (1984): The population of buried viable seeds in relation to contrasting pasture and soil types. J. Ecol. 36: 149-173.
- Chippindale, H.G., Milton, W.E.J. (1934): On the viable seeds present in the soil beneath pastures. J. Ecol. 22: 508-531.
- Colbry, V.L., Swofford, T.S., Moore, R.P. (1961): Tests for germination in the laboratory. In: Seeds. The Yearbook of Agriculture, U.S. Dep. Agr., Washington, D.C. p. 433-443.

- Cook, R. (1980): The biology of seeds in the soil. In: Solbrig, O. (ed.): Demography and evolution in plant populations. Blackwell, Oxford.
- Czimer, Gy., Reiter, J. (1970): A tövises iglice (*Ononis spinosa* L.) keményhéjú magvainak szerepe a legelők újragyomosodásában. (Role of hardcoated seeds of cammock (*Ononis spinosa* L.) in the reappearance of weeds on pastures. Növénytermelés 19: 55–62.
- Czimer, Gy. (1970a): A hazai előfordulású, keményhéjú magot termő növények ökológiai és rendszertani vonatkozásai. (Ecological and taxonomical relations of plants with hardcoated seeds occurring in Hungary.) KATE, Mosonmagyaróvári Mezőgazdaságtud. Kar Közleményei XIII/5: 3–40.
- Czimer, Gy. (1970b): Resistance of hard-coated seeds of *Convolvulus arvensis* L. to various herbicides. Acta Agronomica Acad. Sci. Hung. 19: 321–329.
- Dechkov, Z. (1975): Weed seeds in the soil of some regions in the central part of the Danubian plain. Rast. Nauki 12: 148–157.
- Donelan, M., Thompson, K. (1980): Distribution of Buried Viable Seeds Along a Successional Series. Biol. Conservation 17: 297–311.
- Dore, W.G., Raymond, L.C. (1942): Pature studies. XXIV. Viable seeds in pasture soil and manure. Sci. Agric. 23: 67–79.
- Egler, F.E. (1954): Vegetation science concepts. 1. Initial Floristic composition. A factor in old field vegetation development. Vegetatio 4: 412–417.
- Ericson, L. (1977): The influence of voles and lemmings on the vegetation in a coniferous forest during a 4-year period in northern Sweden. Wahlenbergia 4.
- Fay, P.K., Olson, W.A. (1978): Technique for Separating Weed Seed from Soil. Weed Science 26: 530–533.
- Fekete, R. (1975): Comparative weed – investigations in traditionally – cultivated and chemically-treated wheat and maize crops. IV. Study of the weed-seed contents of the soils of maize crops. Acta Biol., Szeged 21: 9–20.
- Foerster, E. (1956): Ein Beitrag zur Kenntnis der Selbstverjüngung von Dauerweiden. Z. Acker-u.-PflBau. 100: 273–301.
- Golubeva, I.V. (1962): Some data on the number of viable seeds found in soils under meadow-steppe vegetation. Byull. mosk. Obshch. Ispyt. Priro., Otdel. Biol. 67: 76–89.
- Grime, J.P. (1977): Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Amer. Nat. 111: 1169–1194.
- Grime, J.P. (1979): Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester 222 pp.
- Hayashi, I. (1975): The special method of inventory of buried seed population of weeds. Workshop on Research Methodology in Weed Science 1/4.
- Hayashi, I., Numata, M. (1968): Ecology of pioneer species of early stages in secondary succession. II. The seed production. Bot. Mag., Tokyo 81: 55–66.

- Hayashi, I., Numata, M. (1971): Viable buried-seed population in the Miscanthus- and Zoysia-type grasslands in Japan-ecological studies on the buried-seed population in the soil related to plant succession. VI. Jap. J. Ecol. 20: 243-252.
- Hayashi, I., Pancho, J.V., Sastroutomo, S.S. (1978): Preliminary report on the buried seeds of floating islands and bottom of Lake Rawa Pening, Central Java. Jap. J. Ecol. 28: 325-333.
- Hopkins, M.S., Graham, A.W. (1983): The species composition of soil seed Banks Beneath Lowland Tropical Rainforest in North Queensland, Australia. Biotropica 15: 90-99.
- Hopkins, M.S., Graham, A.W. (1984): Viable soil seed banks in disturbed lowland tropical rainforest sites in North Queensland, Australian J. Ecol. 9: 71-79.
- Howe, C.D., Chancellor, R.J. (1983): Factors Affecting the Viable Seed Content of Soils Beneath Lowland Pastures. J. Appl. Ecol. 20: 915-922.
- Hunyadi, K., Pathy, Z. (1976): Keszthely környéki rétláp talajok gyommag fertőzöttsége. (Weed infection of soils of bogs near Keszthely.) Növényvédelem 12: 391-396.
- Hyde, E.O.C., Suckling, F.E.T. (1953): Dormant seeds of clovers and other legumes in agricultural soils. NZ. J. Sci. Technol. 34: 375-385.
- Jensen, H.A. (1969): Content of Buried Seeds in Arable Soil in Denmark and its Relation to the Weed Population. Dansk Botanisk Arkiv 27: 1-56.
- Jerling, L. (1983): Composition and viability of the seed bank along a successional gradient on a Baltic sea shore meadow. Holarctic Ecology 6: 150-156.
- Jones, R.M., Evans, T.R. (1977): Soil seed levels of *Lotononis bainesii*, *Desmodium intordum* and *Trifolium repens* in subtropical pastures. J. Aust. Inst. Agric. Sci. 43: 164-166.
- Keeley, J.E. (1977): Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. Ecology 58: 820-829.
- Livingston, R.B., Allessio, M.L. (1968): Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts, Bulletin of the Torrey Bot. Club 95: 58-69.
- Major, J., Pyott, W.T. (1966): Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13: 253-282.
- Malone, C.R. (1967): A Rapid Method for Enumeration of Viable Seeds in Soil. Weeds 15: 381-382.
- Máthé, I., Précseyi, P. (1971): Újabb adatok az újszentmargitai IBP mintaterület szántóföldjének primér produktiójához. (New contribution to primary productivity examinations of arable fields in the IBP sample area at Újszentmargita.) Agrártud. Közlemények 30: 451-463.
- Milton, W.E.J. (1939): The occurrence of buried viable seeds in soils at different elevations and in a salt marsh. J. Ecology 27: 149-159.
- Milton, W.E.J. (1948): The buried viable seed content of upland soils in Montgomery shire. Empire J. Exp. Agr. 16: 163-177.

- Nakagoshi, N. (1985): Buried viable seeds in temperate forests. In: White, J. (ed.): The Population Structure of Vegetation. Dr. W. Junk Publishers, Dordrecht. pp. 551-570.
- Numata, M., Hayashi, I., Kumura, T., Oki, K. (1964): Ecological studies on the buried-seed population in the soil as related to plant succession. I-II. Jap. J. Ecol. 14: 207-215, 224-227.
- Oosting, H.J., Humphreys, M.E. (1940): Buried viable seeds in a successional series of old field and forest soils. Bull. Torrey Bot. Club 67: 253-273.
- Prince, F.S., Hodgdon, A.R. (1946): Viable seeds in old pasture soils. N.H. Agr. Exp. Sta. Tech. Bull. 89: 3-16.
- Rabinowitz, D. (1981): Buried viable seeds in a North-American tall grass prairie: the resemblance of their abundance and composition to dispersing seeds. Oikos 36: 191-195.
- Rabinowitz, D., Rapp, J.K. (1980): Seed rain in a North American grass prairie. J. Appl. Ecol. 17: 793-802.
- Rabotnov, T.A. (1969): Plant regeneration from seed in meadows of the USSR. Herbage Abstr. 39: 269-277.
- Rabotnov, T.A. (1978): On coenopopulations of plants reproducing by seeds. In: Freysen, A.M.J. and Woldendorp, J.W. (eds): Structure and Functioning of Plant Populations. North-Holland Publishing Company, Amsterdam-Oxford-New York, 1-23.
- Roberts, H.A. (1981): Seed banks in soil. Advances in Appl. Biol. 6: 1-55.
- Roberts, H.A., Chancellor, R.J. (1986): Seed banks of some arable soils in the English midlands. Weed Res. 25: 252-257.
- Roberts, H.A., Dawkins, P.A. (1967): Effect of cultivation on the numbers of viable weed seeds in soil. Weed Res. 7: 290-301.
- Roberts, H.A., Ricketts, M.E. (1979): Quantitative relationships between the weed flora after cultivation and the weed population in the soil. Weed Res. 19: 269-275.
- Schermann, S. (1966): Magismeret I-II. (Atlas of seeds I-II.) Akadémiai Kiadó, Budapest.
- Thompson, K. (1986): Small-Scale Heterogeneity in the Seed Bank of an Acidic Grassland. J. Ecol. 74: 733-738.
- Thompson, K., Grime, J.P., Mason, G. (1977): Seed germination in response to diurnal fluctuations of temperature. Nature, London 267: 147-149.
- Thompson, K., Grime, J.P. (1979): Seasonal variation in the seed banks of herbaceous species in contrasting habitats. J. Ecol. 67: 893-921.
- van der Valk, A.G., Davis, C.B. (1978): The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322-335.
- Virágh, K. (1982): Vegetation dynamics induced by some herbicides in a perennial grassland community. I. Acta Bot. Acad. Sci. Hung. 28: 427-447.
- Virágh, K., Fekete, G. (1984): Degradation stages in a xeroseries: composition, similarity, grouping, coordination. Acta Bot. Hung. 30: 427-459.

- Virágh, K. (1987): The effect of herbicides on vegetation dynamics. A five year study of temporal variation of species composition in permanent grassland plots. Folia Geobot. Phytotax, Praha 22: 46-59.
- Zelenchuk, T.K. (1961): The content of viable seed in meadow peaty soils of the L'vov region. Byull. mosk. Oshch., Ispyt. Prir., Otdel. Biol. 66: 77-92.

EL EFECTO ECOLÓGICO DE LA ROCA SERPENTINA A LA FLORA Y VEGETACIÓN DE CUBA

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A multidirectional approach for understanding the main ecological effects of the serpentine on the flora and vegetation is intended. For introduction a short survey of the soil types, their classifications and the main correlations between soils and vegetation types are given. The ecological importance of the different serpentine factors are widely discussed, then a dynamic concept about the mechanism of the complex serpentine effects on the flora and vegetation is proposed, with several concrete examples selected from the flora and vegetation of Cuba. Size, age and composition of serpentine areas as factors stimulating speciation and isolation of serpentine floras is dealt with, with a special emphasis to the evolution of serpentine endemics. A model of soil and flora evolution is also presented. The main effects of serpentine to tropical vegetation provoking sclerophyllous, microphyllous etc. plant communities of slow metabolism and low intensity of competitive activity are discussed, as well as the descendance or/and inversion of vegetation belts on serpentine. Influence of serpentine on the chorology and area types of cryptogams and phanerogams is also treated. Pseudoxeromorphism or peinomorphy of serpentine vegetation as a general adaptive response to different deficiency stresses is stressed.

BREVE RESEÑA DE LAS RELACIONES EXISTENTES ENTRE LOS SUELOS Y VEGETACIÓN DE CUBA

Constitución geológica

La riqueza de la flora de Cuba y la variedad de su vegetación esta en correlación, en gran medida, con las considerablemente variadas condiciones edáficas del archipiélago cubano. Esto se explica por estar la Isla de Cuba constituida por muchos tipos de rocas (calizas de edad variada, dolomitas, serpentinitas, areniscas, pizarras, así como de basaltos, granitos, granodioritas, dioritas, piroxeno-andesitas, andesitas, gabros etc.), sobre los cuales y a causa de un complejo pasado geológico, se

realizaron variados procesos de desarrollo de los suelos, que tuvieron distinta duración. Por otra parte, unas áreas: como las sierras de Nipe, Cristal, Moa y Baracoa desde el oligógeno han estado constantemente aisladas, mientras una gran parte de las llanuras y de las zonas costeras es bastante joven, pues datan del periodo cuaternario. Es comprensible, que los diversos procesos de desarrollo a que estuvieron sometidos, causaran la formación de diversos tipos de suelos en variadas cantidades y extensión.

Clasificación de suelos de Cuba según Bennett y Allison

Se han preparado 3 obras sinópticas acerca de los suelos de Cuba, realizadas desde diversos puntos de vista. La primera es el libro de BENNETT y ALLISON (1928) que cuenta con un mapa edáfico anexo, realizado a escala 1:1 000 000, de BENNETT (1932). Esta clasificación se basa, principalmente, en caracteres morfológicos (color, estructura, consistencia, características químicas más importantes, presencia de mocarrero o de un horizonte gleyzado acementado, drenaje, origen geológico etc.). Los autores investigaron los suelos de las áreas agrícolas y agropecuarias; mientras los territorios de los bosques, en su mayor parte, quedaron fuera de sus estudios. Clasificaron los tipos de suelos en series y las series en familias parecidamente a un sistema taxonómico botánico o zoológico. El sistema de suelos de Cuba de acuerdo a BENNETT trata 15 familias y 108 series, las cuales llevan los nombres de las localidades geográficas, donde colectaron cada muestra típica del correspondiente suelo (p.e.: familia Matanzas, Nipe, Truffin, Bayamo, Esmeralda, Habana, Norfolk etc.). Su mapa contiene — con algunas integraziones — la distribución de 79 tipos.

El concepto genético de Zonn

ZONN (1968) y anteriormente ZONN, VÁZQUEZ y CABRER-MESTRE (1966) mediante sus análisis propios, apoyándose en los de otros autores, principalmente húngaros (KLIMES-SZMIK, SZABÉDI), elaboraron un sistema genético de los suelos que se basa en su estado de desarrollo evolutivo. Esto, ante todo, puede ser medido en las relaciones moleculares características del suelo y de la fracción arcillosa, en las proporciones moleculares de $\text{SiO}_2/\text{R}_2\text{O}_3$, $\text{SiO}_2/\text{Al}_2\text{O}_3$, $\text{SiO}_2/\text{Fe}_2\text{O}_3$ y $\text{Al}_2\text{O}_3/\text{Fe}_2\text{O}_3$. Su sistema consta de 6 grupos de los tipos de suelos y 17 tipos dentro de estos:

I. Suelos ferralíticos rojos

1. Suelos ferralíticos rojos carbonáticos
2. Suelos ferralíticos rojos ácidos

- II. Suelos cuarzo-alíticos
 - 3. Suelos cuarzo-alíticos humificados
 - 4. Suelos cuarzo-alíticos lixiviados
 - 5. Suelos cuarzo-alíticos y pseudogleyzados
 - 6. Latosoles pseudopodzólicos
 - 7. Suelos cuarzo-alítico-ferríticos amarillos pseudopodzólicos
- III. Suelos formados en serpentinita
 - 8. Suelos ferríticos
 - 9. Suelos ferralíticos
 - 10. Suelos pseudopodzólicos magnesio-sialíticos humificados
- IV. Suelos humico-carbonatados sialíticos
 - 11. Calizos humico-carbonatados
 - 12. Suelos ferralito-calcicos
- V. Suelos pardos sialíticos
 - 13. Suelos pardos carbonáticos
 - 14. Suelos pardos lixiviados
- VI. Suelos oscuros o aluviales
 - 15. Suelos oscuros carbonato-sulfáticos
 - 16. Suelos negros lavados
 - 17. Suelos humicos gleyzados

No se ha realizado el mapa sobre la distribución de los tipos de suelos antes listados.

Primera clasificación genética de los suelos confeccionada por
pedólogos cubanos

El Instituto de Suelos de la Academia de Ciencias de Cuba bajo la dirección de O. ASCANIO, J.N.P. JIMENEZ y A. HERNANDEZ elaboraron un sistema detallado de los tipos genéticos para los suelos de Cuba (1968), el cual, en su concepción, se parece al anterior, pero en el se da más importancia a las particularidades del génesis de los suelos a su morfología y a la calidad de la roca madre. Este sistema contiene 17 tipos principales, dentro de estos, 100 tipos genéticos, según el origen del tipo o la calidad de la roca madre. Estos son los siguientes (entre paréntesis se hace constar la cantidad de los tipos): 1. Latosoles (4), 2. Latosólicos (20), 3. Arenas grises débilmente gleyzadas (1), 4. Negros tropicales (4), 5. Pardos tropicales (18), 6. Calizos pardos y rojos (9), 7. Calizos humificados (8), 8. Praderas tropicales (17), 9. Suelos aluviales (1), 10. Mocarreros (4), 11. Suelos montañosos rojo-amarillentos (7), 12. Suelos montañosos amarillos (2), 13. Turba (1), 14. Suelos cenagosos (1), 15. Ciénaga costera (1), 16. Suelos salinos (1), 17. Carso llano o piedra hueca (diente de perro) (1).

En el año 1968 se realizó un mapa a escala de 1:250 000 y uno de 1:1 000 000 sobre la distribución de estos tipos.

Tipos de suelos que incluye

Las unidades de la 3 clasificaciones mencionadas, en parte son semejantes o coinciden; esto se demuestra en la tabla No. 1. en la cual presentamos algunos ejemplos de los correspondientes tipos

Tabla 1

BENNETT	ZONN	ASCANIO y otros
Matanzas	Suelos ferralíticos rojos ácidos	Latosólico rojo
Nipe	Suelos ferralíticos	Latosoles
Bayamo	Suelos humico-carbonático sialítico	Negro tropical
Guantánamo	Suelo carbonático pardo	Calizo pardo
Mocarrero	Latosoles pseudopodzólicos	Mocarrero
Guane	Suelos cuarzo-alíticos lixiviados	Latosólico amarillo

Dos clasificaciones de suelos más recientes

En el Primer Simposio del Instituto de Suelos de la Academia de Cuba (1975) presentaron dos clasificaciones nuevas. Una de ellas elaborada por TATEVOSIAN, HERNANDEZ, OBREGÓN y otros: "Segunda clasificación de suelos genética de Cuba" es más moderna, más detallada de la primera, sobre todo, en cuanto a la clasificación de los suelos esqueléticos, rendzinas, aluviales, cenagosas, vertisoles y pardos tropicales. La otra clasificación realizada por ASCANIO, sirve para la determinación diagnóstica muy aplicada y caracterización de suelos para la práctica de la agricultura. Esta última une en una forma explicativa la base teórica de la pedología genética con los requerimientos de la práctica agraria. También ayuda grandemente al ecólogo en el reconocimiento rápido de los más importantes tipos de suelos.

Notas ecológicas sobre las clasificaciones de suelos de Cuba

Las clasificaciones mencionadas — basadas en análisis e investigaciones correctas y detalladas — indican al ecólogo y al pedólogo, que la gran mayoría de los tipos clasificados representa perfiles incompletos, decapitados, erosionados o por lo menos modificados por la influencia

antrópica de muchos siglos. Esto aparece muy significativamente, cuando comparamos perfiles en ecosistemas naturales con los descritos por BENNETT, ZONN etc. Estos perfiles descritos se encuentran muy raramente bajo una vegetación natural. TATEVOSIAN (Simposio del Instituto de Suelos, 1975) expresó que los suelos cubanos son mayormente tipos muy viejos, caracterizados por una permeabilidad lenta y escasa, por una acumulación grande, por la circulación de materiales disminuida y por una baja actividad microbiológica. Desde el punto de vista ecológico, estas características no indican necesariamente la vejez del suelo, A mi juicio, los bosques tropicales de distintos tipos predominaron originalmente en casi todo el territorio de Cuba (BORHIDI 1974, BORHIDI y HERRERA 1977, BORHIDI y MUÑOZ 1980, 1984) sobre suelos silvestres caracterizados por un horizonte A más o menos rico en materias orgánicas y humificadas. Después de la intensa tala y quema de los bosques este estrato superior se descompuso en parte y en su mayoría se perdió por la erosión. El horizonte A actual es el producto de una sucesión secundaria y se ha formado del estrato superior del horizonte B original que ocupó de esta manera la superficie y se ha reactivado debido a la larga sucesión secundaria provocada por la influencia de las sabanas semiantrópicas y antrópicas. Este nuevo horizonte A constituye una capa estrecha y más pobre en nutrientes y materias humificadas de lo que fue el original. Tiene características físicas y químicas menos favorables y más baja fertilidad, permeabilidad y actividad biológica. La diferencia entre los horizontes A actual y original es causada también por la menor producción de biomasa de las sabanas, y también por las consecuencias desfavorable pedozoológicas microbiológicas de la quema repetida. Pues tengo la opinión que los suelos de las llanuras cubanas deben considerarse como suelos deteriorados por el hombre, degradados o por lo menos modificados y no son suelos muy antiguos, — salvo algunos latosoles de serpentinita. Sobre los suelos de los bosques tenemos pocas informaciones todavía.

ALGUNAS RELACIONES ENTRE SUELOS Y VEGETACIÓN

Tipos de suelos — tipos de vegetación

Al comparar el mapa genético de los suelos de Cuba y el mapa de vegetación potencial (BORHIDI y MUÑOZ 1980, 1984) se puede determinar muchas diferencias y paralelismos. Primeramente, que el número de los tipos de suelos es mucho mayor que el de tipos de vegetación, así pues, la



Fig. 1. Sabana serpentínica secundaria, considerada por LEÓN como original, en San Serapio, prov. Camagüey, con palmas endémicas (Foto: A. BORHIDI)

calidad del suelo no siempre es el factor determinante en la formación de la vegetación. Los tipos de vegetación climax son sensibles solamente a cambios abruptos entre suelos muy diferentes. El climax es capaz de compensar diferencias edáficas menos notables.

Tipos de suelos sobre serpentinita

Se ve claramente que la serpentinita, dentro de cada tipo de suelo, forma un tipo de vegetación distinto respecto al que se desarrollaría en otra roca basal. La influencia de la serpentinita se manifiesta en todos los tipos genéticos de suelos, aunque poco en los pardos tropicales. Es de notar que en los suelos latosólicos se pueden formar muy distintos tipos de vegetación, mientras algunas formaciones vegetales, como los bosques semidecíduos o los pinares pueden desarrollarse en tipos de suelos muy diferentes. Las relaciones suelo-vegetación resumidas en el párrafo siguiente, no son obligadas pero se presentan, con gran frecuencia.



Fig. 2. Matorral serpentinoso, la vegetación original en San Serapio, prov. Camagüey (Foto: A. BORHIDI)

Relaciones frecuentes entre suelos y vegetación

Se puede afirmar, que los pinares y las pluvisilvas montanas esclerófilas crecen con gran probabilidad en los latosoles y los suelos cuarzo-alíticos y arenosos grises, pobres en nutrientes, son cubiertos también mayormente por pinares. En los suelos serpentinosos sialíticos o alito-ferríticos (esqueléticos) crecen matorrales siempreverdes, o espinosos secos, mientras que en las calizas una vegetación de estructura similar crece sobre suelos húmicocarbonáticos pardos (rendzina tropical). En los suelos negros tropicales la vegetación original está formado por bosques aluviales, al igual que en las praderas tropicales — según esta clasificación — que originalmente también estaban cubiertas por bosques. Los suelos pardos tropicales, en su mayor parte, estuvieron cubiertos por bosques semidecíduos, mientras en los latosólicos rojos la vegetación original

típica era el bosque siempreverde estacional de llanura y el bosque semideciduo tropical. En los suelos rojo-amarillentos encontramos las pluvisilvas tropicales submontanas, mientras que las pluvisilvas montanas húmedas y los bosques nublados que corresponden a la ceja de los Andes viven, por lo general, en suelos tropicales amarillos. Los mocarreros, a pesar de sufrir la fluctuación intensa del nivel freático no estaban cubiertos por sabanas originales, como lo supusieron BENNETT y ALLISON (1928). La capa vegetal original de los mocarreros era un matorral o un bosque arbustoso espinoso deciduo o semideciduo, que se convierte rápidamente en sábanas a consecuencia de la quema, y su repoblación por bosque se realiza muy lentamente. Por eso en los mocarreros, por lo general, encontramos sabanas semiantropicas con palmas de los géneros Sabal y Copernicia, o maniguas secundarias de marabú (Dichrostachys cinerea).

En las lomas del carso cónico (mogotes) dominan los bosques arbustosos deciduos especiales o los bosques semideciduos micrófilos, que se denominan bosques de mogote. El tipo de carso llano desnudo, llamado piedra hueca o diente de perro, también, está cubierto por un mosaico de bosques semideciduos, deciduos y esclerófilos secos. La vegetación costera está bastante rigurosamente determinada por la calidad geológica de la costa. En las playas arenosas encontramos una vegetación especial característica, mientras en las costas rocosas, altas (seborucos) crece un matorral espinoso, mayormente esclerófilo, con endémicos aislados. Las costas bajas, fangosas están cubiertas por manglares. En las cuencas bajas de mal drenaje se desarrolla una vegetación cenagosa, con herbazales de ciénaga, bosques de ciénaga siempreverdes y deciduos. A lo largo del borde interior de los manglares se extienden suelos extremadamente salinos, cubiertos por una vegetación baja formada por arbustos y semiarbustos suculentos y enanos. La tabla 2 muestra las relaciones mas frecuentes entre las formaciones vegetales y tipos de suelos, teniendo en cuenta la nomenclatura de distintas clasificaciones de suelos de Cuba, publicados en 1973, 1975 y 1979 respectivamente (según CAPOTE y BERAZAIN 1985).

Tabla 2

Relaciones entre tipos de suelos y los de vegetación según
Capote y Berazain 1985

Formación vegetal	1973	1975	1979
1. Formaciones arbóreas:			
Bosques:			
I.1. Bosque pluvial:	Latosólico	Ferralítico	Ferralítico
I.1.1. de llanuras	Amarillo tropical	rojo	rojo
I.1.2. montano	Latosólico	Ferralítico	Ferralítico
	Amarillo tropi- cal	amarillento lixiviado	amarillento lixiviado
		Ferralítico	Ferralítico
		rojo	rojo
		Ferrítico	Ferrítico
		púrpura	púrpura
I.2. Bosque nublado	Latosólico	Ferrítico	Ferrítico
	Latosol	púrpura	púrpura
	Amarillo tropical	Ferralítico	Ferralítico
		amarillento	amarillento
		lixiviado	lixiviado
I.3. Bosque siempreverde			
I.3.1. mesófilo	Latosólico	Ferralítico	Ferralítico
	Amarillo tropical	rojo	rojo
	Pardos	Fersialítico	Fersialítico
		pardo-rojizo	pardo-rojizo
		Paro	Fersialítico
			rojo-amari- llento
			Pardo con carbonatos
I.3.2. micrófilo	Calizos humi- ficados	Rendzina roja	Rendzina roja
		Rendzina negra	Rendzina negra
I.4. Bosque semideciduo			
I.4.1. mesófilo	Calizos humi- ficados	Rendzina roja	Rendzina roja
	Pardos	Rendzina negra	Rendzina negra
		Pardo con diferenciación de carbonatos	Pardo con carbonatos
I.4.2. micrófilo	Esquelético sobre piedra hueca	Esquelético	Protorendzina negra
			Protorendzina parda
			Esquelético

Tabla 2
(continuación-2)

Formación vegetal	1973	1975	1979
I.5. Bosque de ciénaga	Gley tropical	Pantanosos	Cenagosos (1)
I.6. Bosque de galería	Aluvial	Aluvial	Aluvial
I.7. Bosque de mangles	Gley tropical	Pantanosos	Cenagosos (1)
I.8. Bosque de pinos	Latosol Latosólico Amarillo tropical Pardo tropical	Ferrítico púrpura Ferralítico cuarcítico Esquelético	Ferrítico púrpura Arenoso cuarcítico Ferralítico cuarcítico amarillento Esquelético
II. Formaciones arbustosas:			
Matorrales:			
II.1. Matorral xeromorfo costero y sub-cos- tero	Esquelético sobre piedra hueca Pardos	Esquelético Rendzina roja Rendzina negra Pardo con diferenciación de carbonatos	Esquelético Rendzina roja Rendzina negra Pardo con carbonatos
II.2. Matorral xeromorfo espinoso sobre serpentina	Pardo tropical	Fersialítico pardo-rojizo	Fersialítico pardo-rojizo
II.3. Matorral xeromorfo sub-espinoso sobre serpentina	Latosol Pardo tropical	Ferrítico púrpura Fersialítico pardo-rojizo	Ferrítico púrpura Fersialítico pardo-rojizo
II.4. Matorral sub-alpino	Pardo amarillen- to montañoso	(2)	(2)
III. Formaciones herbáceas:			
III.1. Comunidades acuáticas de aguas dulces (3)			
III.2. Comunidades halófitas	Suelos salinos	Solonchak Solonetz	Solonchak Solonetz
III.3. Herbazal de ciénaga	Gley tropical	Pantanosos	Cenagosos (1)
III.4. Herbazales de orillas de ríos y arroyos	Aluvial	Aluvial	Aluvial
IV. Complejos de Vegetación:			
IV.1. Mogotes	Esquelético sobre piedra hueca	Rendzina roja Rendzina	Rendzina roja Rendzina

Tabla 2
(continuación-3)

Formaciones vegetales	1973	1975	1979
IV.1. Mogotes	Calizos humi- ficados Pardos la- tosólicos	negra Pardo con di- ferenciación de carbonatos Ferralítico rojo	negra Pardo con car- bonatos Ferralítico rojo
IV.2. Vegetación de costa rocosa	Esquelético sobre piedra hueca Calizos humi- ficados	Rendzina roja Rendzina negra	Rendzina roja Rendzina negra Protorendzina negra Protorendzina parda
IV.3. Vegetación de costa arenosa		arenoso carbonatado (4)	
V. Vegetación secundaria:			
V.1. Bosques secundarios (5)			
V.2. Matorrales secundarios (5)			
V.3. Sabanas	Negro tropical	Oscuros plásticos gleyzados Oscuros plásticos gleyzados Oscuros plásticos no gleyzados	Oscuros plásticos gleyzados Oscuros plásticos neoautomórficos Pardo grisáceo
V.4. Vegetación ruderal (5)			
V.5. Vegetación segetal (5)			

NOTAS: (1): Nivel de Agrupación
 (2): Unidades de suelos no descritas
 (3): No se encuentran sobre suelos
 (4): No comprendido en estas clasificaciones
 (5): Sobre todas o casi todas las unidades de suelos

El efecto de la roca serpentina en la flora y la vegetación

El efecto ecológico que la roca serpentina ejercido sobre la flora ha sido analizado en todas las zonas climáticas de la tierra y se la determinado, que las áreas de serpentinita tienen una flora especial y en todas

partes constituyen territorios particularmente interesantes desde el punto de vista de la evolución de las especies y de la conservación de la flora antigua (relicta).

Serpentina y endemismo

RUNE (1953) planteó que las rocas de alto contenido de Ca y Mg (serpentina, magnesita, dolomita, caliza, yeso, gabro) favorecen la formación y conservación de especies paleoendémicas y relictas, mientras que en los suelos ricos en metales pesados se desarrollan, principalmente, los táxones neoendémicos. La serpentinita une estas dos particularidades químicas y por esto las floras de las áreas de serpentinita son ricas en paleoendémicos y en neoendémicos.

Riqueza de especies en las serpentinitas

Segun KITAMURA (1950), RUNE (1953) y WHITTAKER (1954) la riqueza de la flora serpentinicola depende de la extensión del área de la serpentinita y de la riqueza florística de las zonas aledañas, o sea, del espacio y de la capacidad del almacén genético circundante.

La serpentinita como un complejo de los factores ecológicos

Al analizar los mecanismos de la influencia de la serpentinitas, la mayoría de los investigadores apoya la opinión (vea el resumen de KRAUSE, 1958) de que la serpentinita ejerce su influencia ecológica por la combinación de varios factores limitantes equivalentes, la llamada "combinación de serpentinita". Esta combinación es producto de los siguientes factores:

a) Proporción Ca/Mg: BLACKSHAW (1920), NOVAK (1928), BECKETT (1965), PROCTOR (1971a, b), además LYON, PETERSON, BROOKS y BUTLER (1971), consideran determinante la baja proporción de Ca/Mg de los suelos de serpentinita, la que hace peligrar la estabilidad del equilibrio celular interno del calcio y magnesio de los organismos, o mas precisamente limita el desarrollo de este equilibrio. La proporción de Ca/Mg en los suelos jóvenes sobre serpentinita en Cuba es: 0.01-0.5, ni siquiera en los latosoles más maduros alcanza el valor de 1. Este factor es probablemente muy importante y aclara el por qué la serpentinita implica biótotos insoportables para otras plantas tolerantes al magnesio, que viven por ejemplo, en dolomita o yeso. A la vez se puede determinar que ni el alto contenido, ni el exceso de Mg son caracteres permanentes de los suelos de serpentinita. BENNETT y ALLISON

(1928) además de ROBINSON, EDGINGTON y BYERS (1935) demostraron, que los latosoles y los latosólicos de serpentinita son prácticamente libres de magnesio. Es indudable que por la inestabilidad del equilibrio del calcio y magnesio, el caracter ultrabásico de los suelos jóvenes de serpentinita de contenido de SiO_2 relativamente bajo, puede cambiar rápidamente. Este cambio rápido causa, en muchos casos, el caracter ecológico bifacial de la serpentinita: que a la vez es relativamente básica y ácida.

b) Pobreza de nutrientes u oligotrofismo: GORDON y LIPMAN (1926) resaltan el papel de los valores altos de pH acompañados por la pobreza en N y P en los suelos de serpentina. SPENCE y MILLAR (1963) acentúan la importancia ecológica del nivel bajo de K, N y P en el suelo. ROBINSON et al. (1935) llaman la atención sobre el lavado del Si durante la evolución del suelo, además de la pobre reserva de Al de las arcillas de la capacidad de absorción condicionada por la falta de Ca. BENNETT y ALLISON señalaron que la arcilla de los latosoles de serpentinita en Cuba tiene una capacidad de absorción 10 veces menor que la fracción arenosa de un loam arenoso. LIPMAN (1926) subraya la pobreza extraordinaria de la microflora de estos suelos.

c) Falta de calcio: KRUCKEBERG (1954) y WALKER (1954) consideran que el papel determinante que desempeña la falta del Ca como factor limitante y lo secundario que resulta el Mg. Sin embargo en el caso de la serpentinita los dos factores son inseparables.

d) El efecto tóxico del magnesio: PROCTOR en sus excelentes estudios (1970, 1971b) señala reiteradamente al fuerte efecto tóxico del Mg. Con sus experimentos comprobó que en proporción baja de Ca/Mg el efecto tóxico del Mg es lo que resulta decisivo. El efecto tóxico más fuerte lo produjo el Mg cuando el Ca faltaba por completo, y con una mínima adición del Ca el efecto toxicante disminuyó notablemente. Así PROCTOR, aproximando el problema al otro lado, reforzó la tesis de KRUCKEBERG y WALKER sobre la importancia de la falta de Ca.

Sin embargo, los estudios de BERAZAIN (1976, 1981) realizados en Cuba, señalan que las plantas serpentínicas logran el equilibrio de la baja proporción de Ca/Mg del suelo mediante un fuerte control de absorción. Ella analizó 6 especies serpentínicas y encontró que el índice en las hojas de todas las plantas estudiadas figuraba cerca o sobre de 1, a pesar de la proporción baja — 0.09–0.17 — de Ca/Mg en los suelos. Entre las 6 especies analizadas el Leucocroton havanensis Borhidi (L. flavicans auct. cub. non Muell. Arg.) se presentó como tolerante de serpentina más eficiente, porque en sus hojas la proporción de Ca/Mg aproxima el óptimo fisiológico (Tabla 3).

Tabla 3

Análisis de contenido de elementos del suelo de serpentinita y de las plantas que viven en ella. Loma Galindo, Prov. Matanzas, Cuba; según BERAZAIN 1981

	Ni	Co	Mg	Fe	Ca	Cu	Zn	Ca/Mg
Latosólico de serpentinita								
Horizonte A:	1.58	0.03	5.81	12.1	1.04	0.00	0.00	0.17
Horizonte B+C	1.29	0.02	11.61	9.9	1.04	0.00	0.00	0.09
Plantas serpentínicas								
<u>Leucocroton</u>								
<u>havanensis</u>	11.45	0.05	7.13	0.18	26.58	0.02	0.05	3.72
<u>Buxus flavi-</u>								
<u>ramea</u>	6.34	0.02	13.75	0.26	18.36	0.02	0.04	1.26
<u>Myrtus matan-</u>								
<u>zasia</u>	0.89	0.03	12.50	0.50	11.60	0.04	0.03	0.92
<u>Neobrachea valen-</u>								
<u>zuelana</u>	0.12	0.01	14.50	0.38	20.78	0.03	0.04	1.43
<u>Ternstroemia</u>								
<u>peduncularis</u>								
<u>ssp. obovalis</u>	0.02	0.01	6.25	0.13	13.34	0.02	0.03	2.13
<u>Coccothrinax</u>								
<u>miraguama</u>								
<u>ssp. roseocarpa</u>	0.05	0.01	2.50	0.18	3.38	0.02	0.06	1.35

e) Falta de molibdeno: Está demostrado por JOHNSON, PEARSON y STOUT (1952) el papel ecológico de la pobreza de los suelos de serpentinita en microelementos fisiológicamente importante, principalmente en Mo.

f) Contenido alto de hierro: Según los análisis de SARASIN (1977), GÖHLERT (1928), MINGUZZI y VERGNANO (1953) este factor juega un importante papel en la provocación del nanismo de las plantas. Es cierto que una de las particularidades más visibles de las plantas serpentínicas es la estatura enana. En los suelos de serpentinita el contenido de Fe_2O_3 se puede elevar hasta 80%. WILTSHIRE (1974) demostró en Rodesia que en plantas resistentes a las serpentinas la acumulación de Al y Fe se elevó a un nivel que resulta tóxico causado por su nutrición con nitratos.

Todas las seis especies estudiadas por BERAZAIN (1981) se detectaron como acumuladores notables de Fe, sin embargo, ninguna de ellas mostró estatura enana en comparación con las demás especies de sus respectivos géneros. Según mis observaciones, el enanismo, en Cuba, se presenta sólo en los latosoles maduros de los territorios de serpentinita más antiguos, donde los suelos contienen más del 50% de Fe_2O_3 (Arcilla de Nipe).

g) El efecto tóxico del níquel: El efecto del alto contenido de Ni en los suelos fue estudiado recientemente por varios autores. HUNTER y VERGNANO (1952), CROOKE y INKSON (1955), CROOKE (1956), SOANE y SAUNDER (1959), PROCTOR (1971a, b), PROCTOR y WOODSELL (1971), BROOKS, LEE y JAFFRÉ (1974), WILTSHIRE (1974) y BERAZAIN (1981) estudiaron la tolerancia al Ni de plantas serpentinícolas de distintos orígenes. Esos autores concuerdan en afirmar que el efecto tóxico del Ni debe considerarse notable, sin embargo las plantas acumulan el Ni en grandes cantidades, además de que la intensidad de la absorción de Ni aumenta en suelos ácidos. HUNTER y VERGNANO suponen que en caso de plantas adaptadas al Ni (p.e. Alyssum Bertoloni) este elemento podría jugar un papel positivo en la fisiología de la planta, tal vez ellas substituyen la falta de Ca mediante el Ni. Esta teoría todavía no ha sido confirmada. Por otra parte WILTSHIRE señaló que la tolerancia no dependía de la cantidad acumulada de Ni sino de localización en las plantas. Las poblaciones más tolerantes acumulan igual cantidad de Ni que las menos tolerantes, pero las primeras lo acumulan principalmente en los raices y dejan pasar poco al tallo.

Las investigaciones de BERAZAIN revelan que las especies de pequeñas áreas acumulan más Ni que los táxones de gran área de distribución. Se sabe también que en las hojas de las palmas apenas se acumulan metales pesados (Tabla 3).

GREGORY y BRADSHAW (1965), PROCTOR (1971b) y WILTSHIRE afirman que la tolerancia al Ni es menos específica que la tolerancia al cobre, y que el cromo y el cobre influyen más efectivamente en el mecanismo de la evolución de las especies que el Ni. Este fue comprobado también por DUVIGNAUD (1959), DUVIGNAUD y PLANCKE (1959), DUVIGNAUD y TIMPERMANN (1959) en Katanga, por JACOBSEN (1967, 1968), WILD (1968, 1970), WILTSHIRE (1974) en Rhodesia y por DREW y REILLY (1974) en Zambia.

h) Efecto disgeógeno: Las serpentinitas condicionadas por su descomposición disgeógena, lentísima, crean formas geomorfológicas abruptas de diseño especial, que tienen espacios microclimáticos extremos y biótopos de competencia baja. De esta forma las serpentinitas ejercen un efecto parecido al de las dolomitas (GAMS 1930, ZÓLYOMI 1942) y de otras rocas disgeógenas, como por ejemplo, las cuarcitas, las areniscas, o las arenas sueltas.

i) Características físicas: Varios investigadores (NOVAK y PELISEK, 1940; BENNETT y ALLISON, 1928; ROBINSON et al., RUNE, LAM, 1927) resaltaron las particularidades físicas características de los suelos de serpentinita,

tales como la poca profundidad, el caracter pedregoso, caliente y seco de la rendzina de serpentinita y al mismo tiempo la elasticidad, gran profundidad y gran capacidad de retención de agua de los latosoles de serpentina etc. Sin embargo, se puede ver, que estas particularidades físicas no explican la baja fertilidad de la serpentinita. Por otra parte, durante la evolución del suelo de serpentinitas sus características físicas cambian profundamente sin que se disminuya la influencia ecológica intensa que ejerce sobre la flora.

j) Papel de la baja competencia: Según KRUCKEBERG (1954) este factor desempeña un papel importante en la evolución de las especies serpentínícolas. Las poblaciones no serpentínícolas de las especies que son capaces de vivir igualmente en serpentinitas y en otras rocas también se agotan y desaparecen más rápido por la competencia reñida, que sufren, mientras que las poblaciones serpentínícolas subsisten aisladamente en las condiciones competitivas disminuidas de la vegetación de las serpentinitas. Se supone que evolucionan muchos endémicos a consecuencia de estos agotamientos de biótupos. Las poblaciones adaptadas a las serpentinitas, por lo general, no son capaces de "regresar" a otras rocas, porque no son capaces de soportar la competencia más aguda que domina en otros suelos. Por esto, en la mayoría de los casos la adaptación a la serpentina es un proceso irreversible. Por esto las áreas de serpentinitas pueden considerarse, mayormente, como islas edáficas terrestres, las que poseen una flora endémica de evolución propia (MASON, 1946).

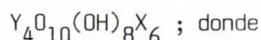
Conclusiones

Basándonos en las observaciones mencionadas, no se puede llegar a una conclusión general acerca del caracter del mecanismo del efecto de las serpentinitas. Las observaciones válidas limitadas para zonas y factores distintos, por el momento, no permiten hacer una conclusión sintética. Sólo se puede asegurar, según KRAUSE (1958), que todos los efectos de las serpentinitas no son caudados por un solo factor destacado, sino por varios. Hay que aceptar la validez, como punto de partida, de una combinación de factores que son fundamentalmente diferentes y en todo caso, hay que escoger y determinar uno por uno sus relaciones de acuerdo con las condiciones del área.

De acuerdo a nuestras observaciones, la determinación antes mencionada puede formularse de manera más concreta: entre todos los factores de

las serpentinitas, lo que efectivamente influye, el factor (o los factores) realmente limitantes, es distinto en dependencia del lugar y del tiempo. Desde el punto de vista del lugar es importante tanto la composición de la roca serpentina (proporción de los minerales arcillosos) como la materia básica de la formación del suelo, y el clima como el factor determinante de la dirección, velocidad y los estadios de evolución del suelo.

La composición química de las serpentinitas es muy compleja y variada, que se refleja de su formula química general siguiente:



$X = Mg^{2+}, Fe^{2+}, Fe^{3+}, Co^{+}, Ni^{2+}, Mn^{2+}, Mn^{3+}, Cr^{3+}, Cu^{2+}, Al^{3+}, Tl^{4+}$, y
 $Y = Si^{4+}, Al^{3+}, B^{3+}, Fe^{3+}$,

además, el OH^- puede ser sustituido por el Cl^- .

La composición de las serpentinitas depende de las relaciones cuantitativas y cualitativas de los minerales arcillosos, que contienen. Los minerales arcillosos más comunes de las serpentinitas son los siguientes:

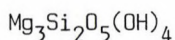
antigorita: $2SiO_2 \cdot 3MgO \cdot 2H_2O$

gentita: $2NiO \cdot 2MgO \cdot 3SiO_2 \cdot 6H_2O$

garnierita: $(NiMg)O \cdot SiO_2 \cdot H_2O$

nepouita: $3(NiMg)O \cdot SiO_2 \cdot 2H_2O$

Las serpentinitas de Oriente — por ejemplo — tienen un mayor contenido de garnierita y nepouita, que las de las demás provincias cubanas (M. FODOR, 1976, comm. pers.). La formula general de los minerales arcillosos de serpentinitas es:



Teniendo en cuenta el número grande de los minerales que constituyen las serpentinitas y la cantidad enorme de los elementos que pueden sustituirse en la composición química, podemos concluir, que practicamente no hay dos formaciones de serpentinitas completamente iguales en cuanto a su composición. En consecuencia de esto los suelos derivados de ellas representan una gran variabilidad también. Mediante esta variabilidad puede explicarse el hecho, que areas de serpentinitas vecinas, donde el aislamiento geográfica no puede jugar un papel muy importante, tienen floras bastante diferentes también, caracterizadas por numerosos endémicos particulares,

como en el caso de las Sierras de Nipe, Cristal y Moa en Norte de Oriente.

El tiempo es importante porque la evolución del suelo se efectúa en el tiempo y en las distintas etapas de la evolución del suelo cambian los factores determinantes de los mecanismos de la limitación y la adaptación.

El único grupo de factores que se mantiene más o menos invariable, independientemente del lugar y el tiempo, es la pobreza en nutrientes. Este factor tiene un gran papel pues el metabolismo de las plantas serpentinícolas es significativamente más lento que el de las plantas crecidas en otras rocas y suelos. Este metabolismo lento es un carácter de adaptación irreversible de las plantas serpentinícolas. Se puede considerar, como una consecuencia de la pobreza en nutrientes, que el aspecto general de la vegetación serpentinícola sea bastante uniforme, a pesar de que los factores ecológicos limitantes pueden ser muy distintos. Sin embargo la oligotrofia de las serpentinitas no puede ser aceptada como el único factor limitante, porque otras rocas oligotróficas pueden producir también una vegetación de fisionomía semejante, pero ninguno es capaz de desarrollar un banco genético tan rico como las serpentinitas. Sin embargo, no se puede menospreciar la importancia del carácter oligotrófico de los suelos de serpentinita, como factor ecológico. Esto fortalece la efectividad de cada uno de los demás factores limitantes que ejercen su influencia ecológica durante las distintas etapas de la evolución del suelo, obligando a las plantas que subsisten a absorber los materiales venenosos y a tolerarlos.

UN CONCEPTO DINÁMICO ACERCA DEL EFECTO DEL COMPLEJO ECOLÓGICO DE LAS SERPENTINITAS SOBRE LA FLORA Y VEGETACIÓN TROPICALES

A continuación trataremos de lograr un concepto general sobre la importancia y orden consecutivo de los diferentes factores ecológicos en cuanto a sus efectos en el mecanismo de evolución de la flora y vegetación tropicales en las áreas de serpentinitas de diferentes climas, extensiones y edades.

Las áreas de serpentinitas de Cuba

El territorio de Cuba es extraordinariamente favorable para el estudio de la evolución y adaptación de las floras serpentinícolas. Encontramos en ella 3 grandes sierras de serpentinitas además de 9 regiones

llanas o colinosas aisladas y de distintas extensiones, con una superficie total de 7500 km². Estos territorios se difieren entre si, en su mayor parte, por tener distintas condiciones climáticas, orográficas, históricas y edáficas. Por esto son útiles para hacer diversas observaciones comparativas. Más adelante daremos un resumen de ellas y al mismo tiempo, ampliaremos o rectificamos las definiciones citadas.

Géneros endémicos de la serpentina de Cuba

Las áreas de serpentinita han resultado los talleres más eficientes de especiación en Cuba. Una tercera parte de la flora endémica de Cuba (920 especies, 31.2%) se evolucionó en las áreas de serpentinitas y viven hoy exclusivamente en estas áreas, que ocupan sólo el 7% del total del territorio de Cuba. De la flora fanerogámica de Cuba, el 14.6% es endémica de las serpentinitas. De los 72 géneros fanerógamicos endémicos de Cuba actualmente conocidos, 24, o sea el 33.3%, son exclusivamente serpentinícolas, que son los siguientes: Sauvallella (Fabaceae), Kodalyodendron (Rutaceae), Moacroton (Euphorbiaceae), Tetralix (Sterculiaceae), Adenoea (Turneraceae), Phidiasia, Sapphoa, Dasytropis (Acanthaceae), Ceuthocarpus, Schmidtottia, Acunaeanthus, Neomazaea, Ariadne, Phyllomelia, Eosanthé, Shaferocharis (Rubiaceae), Koehneola, Lescaillea, Harnackia, Shafera, Ciceronia, Feddea (Asteraceae), Ekmanochloa (Poaceae); así el 75% (3 géneros) de los géneros endémicos de Acanthaceae el 66% (8 géneros) de los géneros endémicos de Rubiaceae y el 50% (6 géneros) de los géneros endémicos de las compuestas son exclusivamente serpentinícolas.

CAUSAS DE LA RIQUEZA FLORAL DE LAS SERPENTINITAS

La riqueza de la flora serpentinícola, según nuestras observaciones, depende de los factores, que a continuación se relacionan en orden de importancia decreciente:

- a) Edad del territorio de serpentinita.
 - b) Extensión del territorio de serpentinita.
 - c) Número de grandes cambios climáticos ocurridos durante los tiempos geológicos.
 - d) Especialización de la flora circunvecina.
 - e) Riqueza de la flora circunvecina.
- a) La riqueza de la flora serpentinícola depende, ante todo, de la



Fig. 3. Adenoa, un género monotípico endémico en las lomas serpentinosas del Norte de Oriente (Foto: A. BORHIDI)

edad del área, como superficie terrestre interrumpidamente expuesta a la atmósfera (no de la edad de la roca). Más exactamente, del tiempo disponible para la evolución de la flora. De las 12 áreas de serpentinitas de Cuba, 4 son superficies muy antiguas: las lomas de Cajálbana y las sierras orientales de Nipe, Cristal y Moa (incluidas las Cuchillas de Toa y Baracoa).

En estas áreas, como consecuencia del proceso de la evolución del suelo durante varios millones de años, dominan los suelos en estado avanzado de la latosolización, que están considerados por muchos autores, como suelos viejísimos, fósiles.

La edad de los latosoles de Cuba, según FINKÓ, KORIN y FORMELL (1967) ha sido estimada en 30 millones de años. Las áreas restantes de serpentinita se encuentran en las regiones llanas y colinosas de Cuba central, las que tienen más o menos 1 millón de años o son más jóvenes. Los suelos de estos son magnesio-sialíticos hómicos o suelos alítico-ferríticos



Fig. 4. Ariadne (Rubiaceae), un género endémico de la área serpentínica del Norte de Oriente (Foto: A. BORHIDI)

poco evolucionados. Las áreas antiguas de serpentinita suman cerca de 4800 km², es decir, el 64% del total de las superficies de serpentinita, mientras que las áreas jóvenes cubren en total 2700 km², o sea, el 36%.

Comparando la flora de las áreas antiguas y jóvenes de serpentinita (Tabla 4), se hace notar que de los 24 géneros endémicos serpentínicos 22 son particularmente exclusivos de las regiones antiguas de serpentinita. Solamente los géneros Moacroton y Acunaeanthus son comunes; las áreas jóvenes no tienen género endémico propio. De las 920 especies serpentínicas endémicas, 792, el 86%, viven en las áreas antiguas, de estos, 750, el 81%, son exclusivamente propias, mientras 42 especies, el 5%, son comunes con

las áreas jóvenes. Frente a esto, las especies endémicas propias de las áreas jóvenes suman el 14% en total.

Tabla 4

Proporción de géneros y especies serpentinícolas endémicos en las áreas antiguas y jóvenes

	Extensión		Géneros endémicos		Especies endémicas	
	km ²	%	número	%	número	%
Áreas antiguas	4800	64	22	91.7	750	81
Áreas jóvenes	2700	36	0	0	128	14
Común	-	-	2	8.3	42	5
Total:	7500	100	24	100.0	920	100



Fig. 5. *Neobraccia valenzuelana* (Apocynaceae), endémico pancubano, característico para la vegetación de todas serpentinas en Cuba (Foto: A. BORHIDI)



Fig. 6. Melocactus matanzanus (Cactaceae), un endémico local de los matorrales serpentinosos, cerca de Matanzas (Foto: A. BORHIDI)

b) La extensión de la región de serpentina desde el punto de vista de la riqueza de la flora; es importante solamente en ciertos casos extremos; esto ocurre cuando es tan pequeña que así se convierte en un obstáculo al aislamiento de las poblaciones nuevas. En las áreas de serpentina mayores de 500 km² y de la misma edad, las diferencias que presentan los climas, orografías y biótupos, pueden ocasionar efectos mucho más eficientes en cuanto a la riqueza de la flora, que la extensión del área. Así pues, la extensión del área es eficiente cuando está acompañada de una gran variación orográfica, que produce una elevada cantidad de biótupos diferentes. Los datos de la tabla 3 se pueden interpretar, de forma tal que se concluya que además de la edad de las áreas, su tamaño también puede jugar un importante papel en la formación de la riqueza de la flora; pero en realidad la importancia de la extensión de la región es pequeña si se compara con la de la edad.

Esta afirmación está ilustrada por la tabla 5 en que se ve que el área de serpentinita antigua de Cajálbana tiene, en su superficie de 70 km²,

dos veces especies endémicas propias que la zona joven de Camagüey, territorialmente 11 veces mayor. La diferencia se hace más significativa por tener la primera 3 géneros endémicos y varios paleoendémicos aislados, mientras los endémicos del área joven son, casi sin excepción, neoendémicos vicariantes.

Tabla 5

Área de serpentinita	Extensión km ²	Géneros endémicos propios	Especies endémicas propias
antigua: Cajálbana	70	3	35
jóven: Camagüey	800	0	16

c) En la evolución y diversificación de la flora juegan un papel muy importante los cambios climáticos, principalmente los cambios frecuentes de épocas climáticas húmedas y secas.

Puede servir como ejemplo la flora de las dos áreas antiguas de serpentinita de las Sierras de Nipe y Moa. El clima de Moa es notablemente más húmedo que el de la Sierra de Nipe. Pero teniendo en cuenta la existencia de los latosoles profundos y de las pluvisilvas montañas extrazonales en la Sierra de Nipe, tenemos que suponer que esta sierra también tenía antes un clima tropical húmedo. Además, los estratos de mocarrero que se presentan en muchas partes en el perfil profundo de la arcilla Nipe, indican cambios repetidos de épocas climáticas húmedas y secas. A este factor histórico se debe que la riqueza florística de la Sierra de Nipe, aunque se la desarrollado en un área notablemente menor en extensión, se acerca a la riqueza asombrosa de la flora de Moa (vea Tabla 6).

Tabla 6

Área	Extensión km ²	Promedio de lluvia anual mm	Géneros endémicos	Especies endémicas
Sierra de Nipe	500	1617	5	151
Sierra de Moa	2500	2314	5	190
Comunes	-	-	6	263



Fig. 7. *Euphorbia munizii* (Euphorbiaceae) un endémico local de las serpentinas antiguas de la Sierra de Moa (Foto: A. BORHIDI)

Tenemos que plantear que la sequía en Cuba es un factor muy importante para la evolución de las especies. Esta relación no es particular de Cuba ya que la dirección principal de la evolución en el reino vegetal es la adaptación a tolerar la sequía. La influencia decisiva de la sequía en la especiación de la flora de Cuba está muy bien demostrada por la figura 9, la cual aclara en cuanto a Cuba que el 68% de los árboles y arbustos nanófilos y el 75% de los leptófilos son endémicos. En las regiones de serpentinita la especiación provocada por la sequía es más notable todavía, porque la sequía fisiológica de los suelos de serpentinita aumenta, de manera notable, la sequía climática.

d) Es natural que las áreas de serpentinita formadas por denudación, desarrollen su propia flora distinta respecto a la flora de las zonas circundantes, como que funciona de una "flora básica" que es fuente del material genético para las serpentinitas y por esto la riqueza genética de esta



Fig. 8. *Paepalanthus brittonii* (Eriocaulaceae) un subarbusto dominante del estrato herbáceo de los pinares de Moa (Foto: A. BORHIDI)

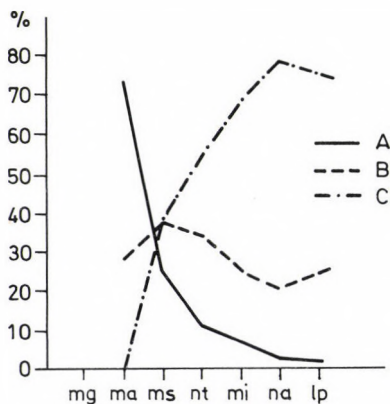


Fig. 9. Repartición porcentual de los árboles y arbustos de la flora de Cuba, según el tamaño de las hojas. — mg = megáfilos, ma = macrófilos, ms = mesófilos, nt = notófilos, mi = micrófilos, na = nanófilos, lp = leptófilos y áfilos; A = especies tropicales, B = especies del Caribe, C = endémicos cubanos

flora básica no carece de importancia. Sin embargo, el grado de especialización de la flora básica, es un factor muy importante respecto a la riqueza en especies de las áreas de serpentinitas receptoras. De una flora básica pobre en especies, pero adaptable, compuesta de taxones genéticamente plásticos se puede desarrollar una flora de serpentinita más rica aún que la flora básica rica, pero ya demasiado especializada. Un ejemplo para esto en Cuba lo tenemos en las lomas de Cajálbana, que están rodeadas por el Sureste, por la zona de calizas del Pan de Guajaibón y por el Sur por los mogotes de la Sierra de los Organos, que están formando superficies terrestres desde la época Cretácica, mientras que las serpentinitas de Cajálbana pueden considerarse como una superficie terrestre existente desde el Mioceno inferior o medio. Así, en esta época la zona caliza ya había tenido una flora especializada durante un largo proceso de adaptación, y sus miembros, en su mayor parte, estaban inhabilitados para la conquista de la región de serpentinita. Por esto Cajálbana no recibió su flora de allí, sino de las Alturas de Pizarra, más pobres en especies; de ellas se desarrollo en Cajálbana, desde entonces, una flora que compite en riqueza y especialización con la flora relictas, antigua de carso cónico de la Sierra de los Organos.

IMPORTANCIA DEL NIVEL DE CALCIO Y MAGNESIO EN LOS SUELOS

Analizando los factores ecológicos que influyen en la evolución de la flora serpentínicola y los que causan su adaptación morfológica característica llamada por "serpentinomorfosis" encontramos, de acuerdo con PROCTOR (1971a, b), que los factores más determinantes son la proporción baja de Ca/Mg y el efecto tóxico de los metales pesados, principalmente, el del Ni. Sin embargo, recalcamos, que estos dos factores generalmente no efectúan sus influencias ecológicas simultaneamente, pues la misma población vegetal, en general, tolera el Mg y el Ni de manera distinta. PROCTOR (1971b: 839), KRUCKEBERG y WALKER (1954) consideran la falta de Ca como el efecto ecológico determinante de la flora de las serpentinitas, luego, la pobreza en nutrientes y finalmente, el contenido alto de Mg y la competencia disminuida. Pero de acuerdo a esto, se convierten en problemáticas las respuestas a varias preguntas, como son, por ejemplo:

a) Por qué podemos encontrar la mayor cantidad de endémicos en los matorrales pioneros crecidos sobre las rendzinas de las áreas antiguas de serpentinita, que aún no son pobres en Ca?

b) Por qué queda aislada genéticamente la flora de las áreas de

serpentinita en los casos en que las circundan zonas de rocas carentes de Ca (como: granita, diorita, arenisca)? Obviamente por el alto nivel de Mg.

Según nuestras experiencias, en las áreas serpentinosas tropicales, — si la composición mineral de la serpentina es conveniente —, la falta de Ca se presenta solamente en los suelos ferralíticos y ferríticos maduros y no en la fase inicial de la evolución del suelo, mientras que el momento determinante de la especialización de la flora serpentínicola se realiza, precisamente, en estos suelos esqueléticos jóvenes, que no son pobres en calcio (contenido de CaO 3–10%) y son ricos en Mg. De aquí que a la falta del Ca, a pesar de ser una particularidad muy notable de los suelos maduros de serpentinita, tenemos que considerarla como de orden secundario o terciario, desde el punto de vista de la evolución de la flora. Es indudable que las especies adaptadas a la falta de Ca son las más apropiadas para establecerse posteriormente en las áreas de serpentinita, — frecuentemente hasta sin cambio biotípico (por ejemplo. Pinus, Poaceae, Ericaceae). Por otra parte las especies acidófilas una vez adaptadas a las serpentinitas formando un biotipo nuevo, mayormente no son capaces de regresar a las áreas con roca basal original, aunque la falta de Ca no sea el obstáculo.

ADAPTACIÓN IRREVERSIBLE Y EL EFECTO DE LA FERTILIZACIÓN EN LA SERPENTINA

La especialización de los árboles y arbustos en la serpentina es mayormente un proceso irreversible, que va acompañando de cambios importantes de sus metabolismos. El obstáculo de la subsistencia de las especies serpentínícolas en suelos de otras rocas no radica solamente en la competencia más elevada que existe en estos suelos. Las experiencias de Julián ACUÑA (comm. pers.) y más las mías propias indican que en el suelo ferrítico de origen no serpentinoso de la antigua Estación Experimental de Agronomía de Santiago de las Vegas, en condiciones exentas de competencia, los endémicos de serpentina transplantados se extinguieron después de un año o dos de vida precaria. Con este mismo asunto se relacionan los experimentos de fertilización con K, N y P realizados en suelos de serpentinita con el objetivo de eliminar su pobreza en nutrientes y alcanzar una mayor productividad de la vegetación. Los fertilizantes provocan aceleración del metabolismo de las plantas causando anomalías en su crecimiento e irregularidades en su desarrollo ontogénico, deshoje y muerte.

Los experimentos de fertilización realizados con gramíneas en suelos de serpentinita, mostraron que el aumento de la cantidad de nutrientes

no era seguido por un aumento significativo de los rendimientos, además, debilita la tolerancia de las plantas a las sustancias tóxicas. La fertilización con Ca resultó la más efectiva (WALKER 1954, PROCTOR 1971b) pero esto en los trópicos puede ser útil solamente en los suelos jóvenes y poco profundos, todavía ricos en Mg. SIMON (1971) encontró en Rodesia, en suelos de alto contenido de Ni y Cr, que las gramíneas utilizadas en el experimento de fertilización no mostraron un mejor, crecimiento a pesar de su absorción intensa de Ca. CROOKE (1956) afirmó que los valores bajos del pH incrementaron el efecto tóxico de los metales pesados. CROOKE e INKSON subrayaron que el efecto tóxico del níquel era más grande en presencia de mucho P, acompañado por un nivel bajo de Ca y K. WILTSHIRE (1974) encontró que las fertilizaciones con N no tuvieron efectos en los suelos de alto contenido de Mg, porque el nitrógeno no modifica la proporción de Ca/Mg. La fertilización con N se ha resultado negativa también en los suelos ricos en Ni porque el amoníaco como fuente de N aumentó el ácida del suelo provocando así una absorción elevada de los metales pesados y el aumento del efecto tóxico (ANTONOVICH, BRADSHAW y TURNER 1971, GIGON y RORISON 1972). Por otra parte, del uso de los nitratos como fertilizantes resultó un aumento de la absorción del aluminio y del hierro hasta un grado tóxico. Además, debemos fijarnos en que estas respuestas vegetales fueron obtenidas estudiando gramíneas de gran adaptabilidad y no en árboles o arbustos menos tolerantes, los que constituyen el 75% de la flora serpentínica de Cuba.

LAS ETAPAS DEL DESARROLLO DE LA FLORA SERPENTÍNICA Y SUS FACTORES ECOLÓGICOS CONTROLADORES

Tomando como base los análisis de la flora serpentínica antigua y extraordinariamente rica de Cuba Oriental, consideramos posible delinear el proceso y las etapas principales de su evolución — si aceptamos por ejemplo un caso simple, donde tenemos un clima húmedo tropical lluvioso durante todo el año, que no ha variado notablemente en el transcurso de la evolución del suelo.

a) Etapa pionera. En esta etapa el factor controlador es la proporción baja de Ca/Mg, o sea el efecto tóxico del Mg. El contenido de CaO de las rendzina jóvenes de serpentinita es del 3-8%, el de MgO puede llegar al 10-40% y la proporción de Ca/Mg varía entre 0.01-0.5. Estos suelos son muy pobres en nutrientes, principalmente en P, y el hábitat se calienta fuertemente, a causa de la estructura abierta de esta vegetación por la

intensa insolación así las plantas tendrían que mover grandes cantidades de agua a través de sus organismos para satisfacer sus requerimientos de nutrición y de transpiración, lo que hace inevitable la admisión de sales de Mg. Puesto que el Mg es un veneno celular que daña el metabolismo y en la serpentinita el biótomo no dispone de la cantidad necesaria de reservas de Ca necesario para lograr equilibrar su efecto, las plantas serpentínícolas tienen que llegar a estructurar un mecanismo interior para un control metabólico riguroso, que hace posible la neutralización del Mg, su eliminación del metabolismo y su almacenamiento. Las plantas que viven en las rendzinas de serpentinita reciben esta suprabundancia del Mg como un verdadero choque ecológico, al cual no tienen posibilidad alguna de acostumbrarse gradualmente; o se adaptan con cambios biotípicos, o se exterminan. Este es el que tenemos que considerar como el momento determinante en la formación de la flora serpentínícola, puesto que por el número y frecuencia de endémicos los matorrales siempreverdes pioneros que cubren las rendzinas de serpentinita (Tabla 6) son los que alcanzan los valores más altos.

Hacemos notar que las plantas ubicuistas, relativamente indiferentes al carácter del suelo, solamente pocas veces son capaces de invadir o establecerse en estos ecótopos pioneros de serpentinita. Para ellos los "ecótopos pioneros" secundariamente formados mediante un proceso de degradación, significan los habitats aptos para conquistar, como podemos verlo en Cuba, en el caso de las invasiones de Dichrostachys cinerea, Rhynchelytrum roseum etc.

b) Etapa de sialitización; efecto de la lixiviación. Durante la evolución ulterior de los suelos de serpentinita, consistente en la sialitización y luego la latosolización, se lixivian gradualmente de Ca y de Mg en los estratos superiores, además disminuye intensamente el contenido de SiO_2 del suelo, y este se acidula. Los minerales arcillosos de tipo montmorillonita van siendo sustituidos por los de caolinita, mientras en el complejo de absorción el Al_2O_3 y el Fe_2O_3 siguen dominando.

El problema del control metabólico de la toxicidad del Mg anteriormente expuesto será sustituido por el de la tolerancia y eliminación de la toxicidad del Al. Es fácil de comprender, que los suelos sialíticos, ferralíticos y sialítico-ferríticos evolucionados en esta forma, tienen características ecológicas fundamentalmente nuevas para la flora serpentínícola ya adaptada a las condiciones de la primera etapa, cuando se habían desarrollando muchos táxones endémicos. Así pues, la nueva etapa de la evolución del suelo, impulsa necesariamente a un otro desarrollo de la flora, que se

realiza en forma de una diferenciación lenta. Para esta etapa la base genética está suministrada por la flora serpentínicola formada ya con anterioridad en las condiciones ecológicas de la primera fase. Fuera de esta flora pionera pueden participar en la formación de la flora serpentínicola de la segunda etapa, las plantas de las zonas de suelos ácidos circundantes, suelos cuarzo-alíticos, suelos montanos amarillos por invasión e intervención genética, refrescando de esta manera los recursos genéticos de las áreas de serpentinitas. Para estas plantas se abre una superficie de penetración en los lugares donde el ritmo de la lixiviación es más rápido que el de la adaptación de la flora local. Como la mayoría de las especies de los matorrales pioneros de serpentina no pueden adaptarse a los suelos sialíticos ácidos de la segunda etapa, las pluvisilvas esclerófilas de serpentina son más pobres en endémicos que los matorrales. Por otra parte la flora de las pluvisilvas esclerófilas se enriquecen con materiales genéticos nuevas las que pueden servir, en el próximo estado de la evolución del suelo, como puntos de partida de una nueva evolución florística; por ejemplo: Talauma minor ssp. minor → Talauma minor ssp. oblongifolia, Cyrilla racemiflora → C. nipensis, Cyrilla cubensis → C. nitidissima, Ilex macfadyenii → I. moana, etc.

c) Etapa de la latosolización. El efecto de los metales pesados. En la última fase de la latosolización, a consecuencia de la lixiviación intensa del SiO_2 y de Al_2O_3 , se desarrollan suelos ferríticos o latosoles, los que se acumulan gran cantidad de Fe_2O_3 , además de óxidos de Ni, Mn y Cr, los que pueden alcanzar un contenido del 60–70% de Fe_2O_3 y del 1.1–1.6% Ni. No es de dudar, que el enriquecimiento de los latosoles, en metales pesados, ejerza una nueva influencia de choque ecológico en las plantas, a pesar de no ser una influencia tan repentina e intensa como la de las rendzinas de serpentinita, sino una tensión ecológica paulatinamente desarrollada. Al ser los latosoles extremadamente pobres en básicos sustituibles (en la arcilla de Nipe es del 1.1%, según BENNETT y ALLISON, 1928), para las plantas es inevitable durante la absorción del agua y también de los nutrientes, al absorber los iones de metales pesados y luego neutralizarlos y almacenarlos, lo que provoca una nueva ola de adaptación. Este proceso se puede observar en el ejemplo siguiente: en los pinares sobre latosoles la frecuencia de los endémicos tiene una tendencia a ser mayor respecto a las pluvisilvas esclerófilas, que es la vegetación zonal de la etapa anterior. Veamos la siguiente tabla:



Fig. 10. Pluviusilva montana esclerófila en la Sierra de Nipe (Foto: A. BORHIDI)

Tabla 7

Frecuencia de endémicos en distintos tipos de la vegetación serpentínicola en el orden de la sucesión

	Matorrales pioneros (4 comunidades)	Pluviusilvas esclerófilas (3 comunidades)	Pinares (6 comuni- dades)	Pinares degradados (3 comunidades)
Endémicos de serpentina en Fr%:	71.65	58.29	63.28	46.67

Como los latosoles tienen varios millones de años de edad pueden haber desarrollado lo que hoy son paleoendémicos y también conservar relictos, como los suelos pioneros ricos en Mg (por ejemplo: Shafera, Koehneola, Feddea, Dracaena cubensis). La tesis de RUNE (1953), que los suelos de los metales pesados inducen, principalmente, el desarrollo de neoendémicos, es válida mas bien en la zona templada holártica, donde la evolución de los suelos se empezó sólo después del último período glaciál. Sin embargo, en



Fig. 11. Pinar abierto sobre serpentina de la Sierra de Nipe, al Norte de la Loma Mensura (Foto: A. BORHIDI)

los trópicos, donde los suelos con muchos metales pesados pueden tener un proceso evolutivo largo, de varias decenas de millones de años; así también sirven como áreas de evolución de una flora rica en paleoendémicos.

SERPENTINA Y COMPETENCIA

Analizando el problema de la competencia, parece que ésta es menos intensa en los latosoles. Los distintos efectos antrópicos, en especial en los pinares de los latosoles, conducen más rápidamente al crecimiento de las plantas indeseables y a la disminución de la flora endémica.

La deriva genética en la evolución de las floras serpentinícolas

Tenemos que señalar que en el mecanismo de evolución de la flora serpentinícola — por lo menos en las condiciones ecológicas de las islas tropicales — la deriva genética (genetical drift) desempeña un papel muy importante. El agotamiento de los bióticos es un proceso que ayuda mucho al aislamiento de los taxones serpentinícolas ya adaptadas durante las distintas fases de la evolución del suelo. Pero en la evolución interior y en la diferenciación genética, o sea en la formación de la riqueza de la flora serpentinícola, la deriva genética juega un papel mucho más importante. Como la vegetación serpentinícola, en su mayor parte, está compuesta por poblaciones entomófilas dispersas, de pocos individuos, es grande la posibilidad y probabilidad de que el nuevo carácter evolucionado se derive de la población principal y se establezca aisladamente. Este proceso está presente en las flóculas particulares de los valles de la Sierra de Nipe, a partir de las poblaciones ancestrales de la meseta se desarrolla en distintas direcciones, así cada uno de los valles tiene sus especies endémicas locales de los géneros Iabebuia, Gochnatia, Calyptanthus, Leucocroton. En las Cuchillas de Moa y Toa, las distintas mesetas y grupos de lomas tienen sus respectivas flóculas propias con abundancia de especies vicariantes de los géneros Cordia, Ilex, Buxus, Phyllanthus, etc.

SERPENTINITA Y VEGETACIÓN

WHITTAKER (1954) analizó la influencia de la roca serpentina en la vegetación en la zona templada, y la comparó con la vegetación de diorita del mismo clima y logró a los siguientes conclusiones:

Características de la vegetación de serpentinita

a) El xeromorfismo o pseudoxeromorfismo, esto consiste en que la vegetación de serpentinita, en cuanto a su aspecto fisionómico, es más

seca, que los tipos de vegetación existentes en otros sustratos geológicos, p.e. en caliza. Según WHITTAKER esto no es solamente consecuencia de las características físicas de los suelos de serpentinita, que frecuentemente pueden ser idénticas a los de otros suelos. La estructura de la vegetación es más abierta, lo que permite la mayor penetración de la insolación, el mayor calentamiento del hábitat, el aumento de la oscilación térmica y de la transpiración. Consecuentemente, la vegetación serpentínicola, en las mismas condiciones de temperatura, tiene una pérdida de agua notablemente más grande que la que crece en diorita.

b) Productividad disminuida. La altura, la densidad de la cobertura y por consiguiente, la producción de biomasa de la vegetación serpentínicola son significativamente más bajas que las de las vegetaciones de otros sustratos geológicos.

c) La disminución del número de los estratos verticales de la vegetación de serpentinita está relacionada con la transmisión de las superficies ecológicamente activas hacia niveles más bajos.

d) Las serpentinitas favorecen al desarrollo de ciertas formas ecofisiológicas (formas de vida), como lo expusó KRUCKEBERG (1954). Las gramíneas tienen ventaja en el establecimiento y distribución en la vegetación herbácea de las serpentinitas, frente a las demás familias; en los bosques, los pinos frente a los árboles deciduos; en las matorrales los arbustos siempreverdes esclerófilos frente a los arbustos caducifolios. Por lo general, la serpentinita favorece la evolución de un tipo de vegetación compuesta por pinos, arbustos siempreverdes y gramíneas.

SERPENTINITA Y SUCESIÓN

La roca de serpentinita influye profundamente en el proceso de sucesión de la vegetación, en las siguientes cuestiones:

a) La serpentinita tiene una serie sucesional especial y un climax propio, que difiere grandemente de los climax de otros sustratos geológicos, y del llamado climax climático.

b) El estado terminal de la sucesión de serpentinita — lo que podemos considerar como climax edáfico — nunca va a llegar a ser una vegetación de igual producción y valor que la de las áreas circundantes no serpentinosas.

El efecto de la serpentinita en la vegetación tropical. Las tesis antes mencionadas, en cuanto al efecto que ejerce la roca serpentinita en la vegetación, deben completarse con los siguientes ideas:

Es indudable, que la roca serpentina tiene series sucesionales y climax edáfico propios, los que se diferencian de las series y climax climáticos producidos por otras rocas basales en climas similares. Sin embargo, respecto a todas las sucesiones en roca serpentina se desarrollan series y tipos de vegetación equivalentes en cuanto a su fisionomías, estructuras y producciones, en otras rocas, pero en climas notablemente más secos. Esto quiere decir que una comunidad vegetal de serpentina representa un grado ecológico más seco respecto a una de caliza o diorita que vive en clima similar, por lo tanto que climas más secos en roca no serpentinosas, se suelen encontrar comunidades de semejantes estructuras, fisionomías y producciones a los de las rocas serpentinas. En Cuba, las series sucesionales de caliza que son equivalentes, desde el punto de vista fisionómico y de producción, a series de rocas serpentinas se desarrollan generalmente, en climas bixéricos, con un promedio de lluvia anual de 400–500 mm menos que las series pendientes en serpentinas y con estaciones secas de 2–3 meses más largas que aquellas. Esta diferencia ecológica causada por el efecto de las rocas serpentinas se manifiesta, en una forma muy ilustrativa, en un diagrama (Fig. 12.) donde comparamos el índice foliar (índice general del tamaño de hojas – I_f) de asociaciones serpentinícolas y de calizas, en relación al promedio anual de lluvia.

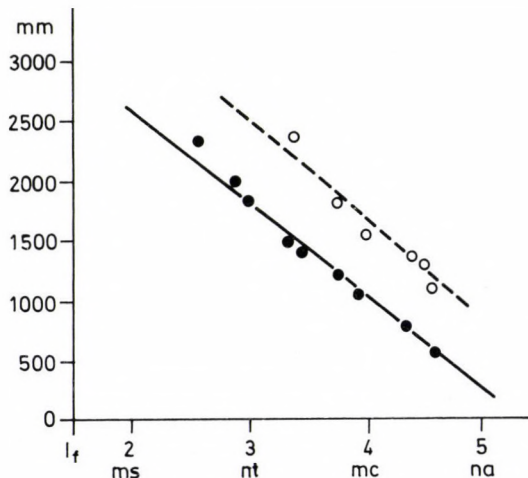


Fig. 12. Valores del índice foliar de distintas comunidades de bosques sobre caliza (puntos sólidos) y sobre serpentina (círculos), en climas húmedos y secos (BORHIDI, original)

Se puede determinar también que en sustratos geológicos ácidos y pobres en nutrientes las series sucesionales son más semejantes a las de las rocas serpentinas. Por ejemplo la vegetación de pizarra y la de arena blanca se desarrollan en respecto a las serpentinas climas más lluviosos, en unos 100–200 mm de precipitación anual y con un período seco solamente un mes más largo, que el de la vegetación de roca serpentina equivalente.

La xeromorfia de la vegetación de serpentina y su equivalencia climática

Esto significa, que el grado del xeromorfismo de la vegetación de serpentina, o sea el de sequía fisiológica de los suelos de serpentina se puede expresar con bastante exactitud de acuerdo a su equivalencia al déficit de la lluvia y a la duración del período seco. Recalcamos que la cantidad de lluvia antes mencionada no solo expresa teóricamente la diferencia en la humedad de los hábitats antes citados, sino que es capaz de compensar la sequía fisiológica de los ecotopos de serpentina. Esto explica la existencia de cayos extrazonales de las pluvisilvas esclerófilas montañas desarrolladas en la zona más seca de los pinares de las Sierras de Nipe y Moa, y también las pluvisilvas húmedas montañas mesoclimáticamente condicionadas en esas localidades de la zona de las pluvisilvas esclerófilas (semisecas) de la Sierra de Moa.

Con respecto a los equivalentes climáticos de la xeromorfia edáficamente condicionada de la vegetación de serpentina y a su compensación climática estudiamos la estructura de las asociaciones vegetales más frecuentes en caliza y serpentina existentes en varios climas, con énfasis especial en el índice general del tamaño de las hojas y en la frecuencia de las plantas espinosas, como características evidentes de xeromorfia de la vegetación. La Fig. 12 muestra las cantidades de lluvia anual que pueden compensar la sequía fisiológica de la roca serpentina, produciendo una vegetación equivalente a la de caliza.

Analizando la frecuencia relativa del clasificador de tamaño de hojas en las asociaciones crecidas en caliza y serpentina respectivamente, según RAUNKIAER, que muestra el grado del xeromorfismo de la vegetación, observamos, que la sequía fisiológica de la serpentina manifestada en el mayor grado del xeromorfismo — más correctamente, en la mayor frecuencia de los individuos micronano-, y leptófilos, es equivalente a un déficit anual de lluvia de 500–600 mm, con la temperatura correspondiente (promedio anual de 24–27 °C). La frecuencia de individuos espinosos, que se manifiesta en

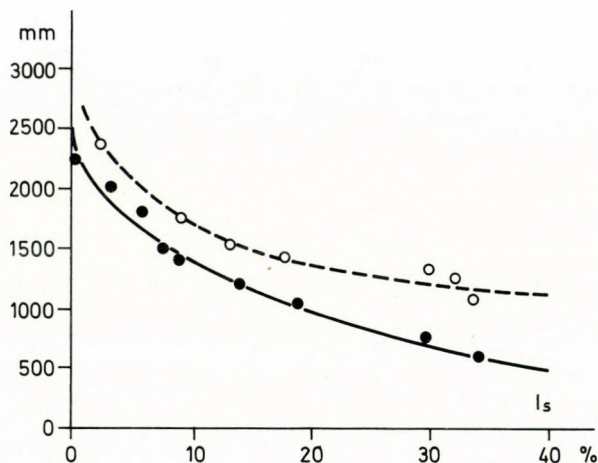


Fig. 13. Valores del índice de espinosidad de distintas comunidades de bosque en caliza (puntos sólidos) y sobre serpentina (círculos) condicionados por climas de lluvia anual diferente (BORHIDI, original)

el índice general de la espinosidad (I_s), demuestra también la xeromorfia elevada de la vegetación serpentínicola. La espinosidad aumenta cada vez más aceleradamente en función de la intensidad y duración de la sequía climática (Fig. 13).

Aprovechamiento del espacio de la vegetación serpentínicola

El deficiente aprovechamiento del espacio vertical y horizontal es característico de la estructura de la vegetación de roca serpentina. Las tesis de WHITTAKER relacionadas con este tema (1954), antes citadas pueden ser completadas con las siguientes observaciones realizadas acerca de la vegetación tropical de Cuba:

La estructura del climax edáfico de las serpentinitas tiene las características siguientes, diferentes de la vegetación del climax climático:

- a) El estrato superior arbóreo o arbustivo es más bajo, con 5-10 m de altura.
- b) El número de estratos de la vegetación es menor en uno.
- c) El estrato superior es siempre abierto.
- d) El estrato activo, cerrado, es el segundo, generalmente el estrato arbustivo.
- e) En la zona de las pluvisilvas se desarrollan pluvisilvas esclerófilas, la que llamamos también semisecas, porque su clima y ecótopos son

húmedos, pero la fisionomía de la vegetación es xeromorfa. La peculiaridad más visible de las pluvisilvas esclerófilas semisecas es que su estrato arbóreo superior es abierto, lo que da como resultado, la falta de algunos estratos inferiores de plantas exigentes a la sombra, por ejemplo el estrato de los epífitos esciófilos; son pobres en orquideas y helechos epífitos, y faltan casi completamente los musgos y hepáticas epífitos y epífilos, además también son pobres en musgos terrestres que están sustituidos, mayormente por líquenes. Al mismo tiempo tienen un estrato arbustivo muy desarrollado, compuesto por arbolitos y arbustos micrófilos (BORHIDI y MUÑIZ 1980).

La extraazonalidad edáfica de la vegetación serpentínicola

Como una conclusión muy importante, debemos plantear, que la vegetación de serpentina, por su estructura laxa y xeromórfica, por su poca productividad, puede considerarse como una representación extraazonal de una zona climática y vegetal más fría. No cabe duda que ciertos tipos de la vegetación serpentínicola, sobre todo los matorrales esclerófilos y los pinares asociados con arbustos siempreverdes esclerófilos, son fisionómicamente muy semejantes a las formaciones de maquis, chaparral y garriga del clima mediterráneo o a los pinares mediterráneos.

Bajada de las zonas vegetales en las montañas de serpentinita

La bajada de la vegetación zonal se hace sentir más claramente en la estratificación de las zonas verticales de la vegetación serpentínicola. LAM (1927), BAUMAN-BODENHEIM (1956) y YAMANAKA (1952) determinaron, que distintas especies de plantas alpinas y montanas son propensas a migrar hacia regiones más bajas en los suelos de serpentinita. Nuestras observaciones hechas en Cuba (BORHIDI y MUÑIZ 1980, 1984), demostraron que no se trata solamente del descenso migratorio de algunos elementos de las montañas altas, sino del descenso de zonas completas de vegetación — o sus variantes más secas; así vemos que en las montañas de serpentinita se desarrollan en una altura mucho más baja respecto al nivel del mar si los comparamos con las montañas que no son de serpentinita. Otro fenómeno interesante de la zonación vertical en la serpentinita es que vegetaciones de las áreas hiperhúmedas, aunque fueran condicionadas climáticamente como la zona del bosque nublado, no desarrollan en las montañas de serpentinita, así quedan completamente fuera de la zonación vertical. Los datos de la Tabla 8 y la figura 14 muestran la distribución de las zonas verticales de vegetación en dos sierras de Cuba oriental (BORHIDI y MUÑIZ 1980, 1984).

Tabla 8

Zonación vertical de la vegetación sobre granodiorita y serpentinita en Cuba

Sierra Maestra (granodiorita)	Sierra de Moa (serpentina)
Bosque siempreverde estacional en alturas de 100–400 m	—
Pluvilsilva submontana en alturas de 400–800 m	Pluvilsilva submontana en alturas de 100–400 m
Pluvilsilva húmeda montana en alturas 800–1600 m	Pluvilsilva esclerófila semiseca en alturas de 400–900 m
Monte nublado en altura de 1600–1900 m	—
Matorral siempreverde subalpino en alturas de 1900–2000 m	Matorral siempreverde montano en alturas de 900–1100 m

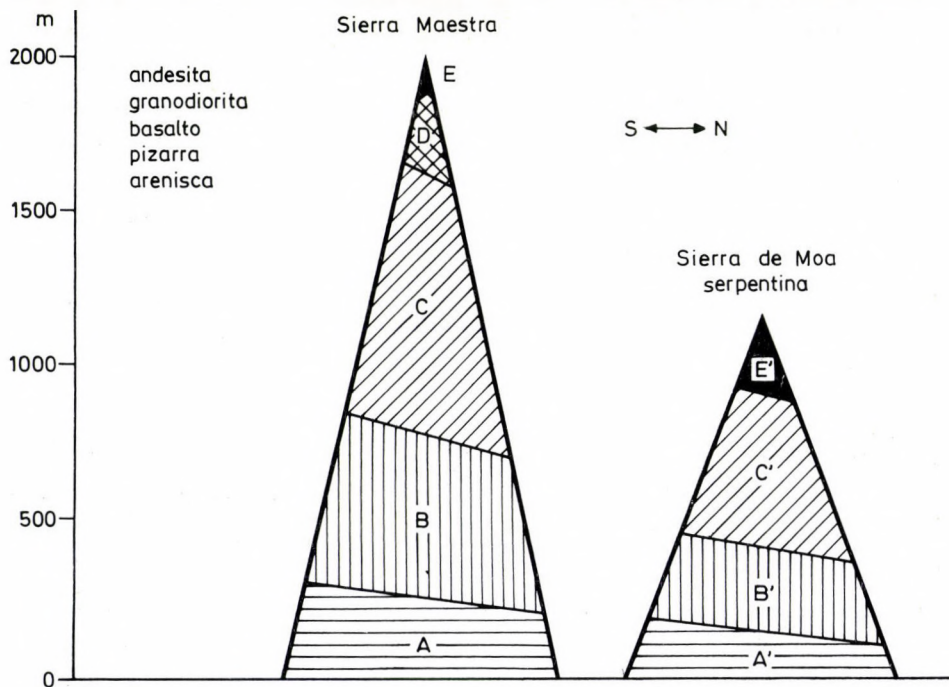


Fig. 14. La zonación vertical de la vegetación climax en dos montañas cubanas de sustrato geológico distinto. — A = Zona de llanos y colinas, B = Zona submontana, C = Zona montana, D = Zona del bosque enano, E = Zona del matorral subalpino

Preferencia de algunos táxones por las serpentinitas

Varios autores han determinado que los suelos de serpentina favorecen ciertos elementos xero-fotófilos y oligotróficos, pertenecientes a los géneros: Pinus, Vaccinium, Genista, Cytisus y a las familias: Myrtaceae, Caryophyllaceae y Gramineae. Según nuestras observaciones y de acuerdo con las de BERAZAIN (1979), en Cuba, los siguientes taxones muestran una preferencia significativa por las serpentinitas (entre paréntesis se brinda el tanto por ciento de las especies serpentínícolas pertenecientes a los géneros y familias relacionados): Podocarpus (4 especies, 80%), Buxus (26 especies, 79%) Harpalyce (16 especies, 94%), Leucocroton (26 especies, 96%), Cyrillaceae (12 especies, 86%), Spathelia (8 especies, 80%), Ossaea (27 especies, 60%), Calycogonium (13 especies, 60%), Ilex (16 especies, 57%).

Efecto de la serpentinita en la flora criptogámica

La serpentinita ejerce un efecto notablemente menor en la diferenciación de la flora criptogámica que en la diferenciación de las plantas fanerógamas. Entre los helechos la proporción de los endémicos es considerablemente menor, mientras que en el país el 30% de los pocos helechos endémicos son serpentínícolas. Algunos géneros de helechos juegan un papel notable en la vegetación de serpentina, como por ejemplo: Anemia, Lindsaya, Pteridium, Odontosoria, mayormente los helechos esclerófilos, rastreros. Frente a esto, el papel de los helechos higrofilos es muy pequeño en la vegetación serpentínícola, por ejemplo, es pequeño el número de helechos arbóreos, epífitos, así como el de las Hymenophyllaceas.

Por el momento, sabemos poco del efecto ejercido por la roca serpentina en los briófitos de Cuba. Estudios realizados en Asia (HATTORI, 1955) no mostraron correlaciones entre la distribución de los briófitos y la de los suelos de serpentinita. Se determinó que en la roca serpentina viven briófitos acidófilos (falta de Ca!), que la proporción de endémicos es relativamente alta, pero estos, en su mayor parte, no son endémicos de serpentina. También se preve para Cuba una tendencia semejante. La tabla 9 muestra las correlaciones de los endémicos con las áreas de serpentinitas. Las áreas de serpentinitas no cubren más de 7% del territorio nacional de Cuba, mientras el 30% de los endémicos no se encuentran fuera de estas áreas, en cuanto a la flora fanerógama. De los pteridófitos 15% de los endémicos vive sobre serpentina, y sólo 10% de los musgos endémicos son serpentínícolas. Con respecto a las hepáticas, ninguno de los endémicos vive



Fig. 15. Leucocroton moaënsis (Euphorbiaceae) una especie endémica de las serpentinas de Moa, vicariante del L. ekmanii de la serpentina de Baracoa (Foto: A BORHIDI)

sobre serpentina. Al nivel genérico las diferencias son todavía más sobresalientes. La flora fanerógama está representada por 24 géneros y 920 especies endémicos de la serpentina, los musgos por ningún género endémico y sólo 4 especies endémicas de la serpentina. Todas las especies endémicas serpentínícolas de los musgos crecen en las áreas de serpentinas antiguas y ninguna en las áreas jóvenes.

Tabla 9

Correlación entre taxones endémicos y áreas serpentinas con respecto a distintos niveles taxonómicos (según Borhidi y Pócs, 1985)

	Territorio nacional de Cuba		áreas de serpentinas	
Superficie	110 922 km ²		7 500 km ²	
Flora	número de especies	% de la flora	número de especies	% de los endémicos
Fanerógamos	6 350	100		
endémicos	3 153	50	920	30
Pteridófitos	500	100		
endémicos	53	11	8	15
Briófitos	723			
Musgos	386			
endémicos	39	10	4	10
Hepáticas	337			
endémicas	cc.17	5	?	?

En general, la flora de briófitos de los suelos de serpentinita es pobre en especies. El desarrollo de una capa terrestre continua de briófitos es muy raro en las serpentinitas incluso en la zona de las pluvisilvas húmedas. La mayoría de las especies serpentínícolas son acidófilas y es relativamente frecuente la presencia del género Sphagnum. Los briófitos epífilos y epífitos desempeñan un papel mucho menos relevante en las pluvisilvas esclerófilas de la serpentina, que de las de otros sustratos geológicos a pesar de que el clima de las áreas serpentinas puede ser más húmeda de lo de las non-serpentinas (Tablas 10 y 11).

Tabla 10

Número de especies criptógamas crecientes en pluvisilvas montañosas serpentinadas y non-serpentinadas respectivamente basado en muestras fitosociológicas 10 de cada una de áreas de 0.25 hectáreas (según BORHIDI in BORHIDI y PÓCS, 1985)

	Pluvisilvas montañosas	
	áreas non-serpentinadas Sierra Maestra	áreas serpentinadas Sierra de Moa
Precipitación promedio anual	2000 — 2500 mm	3000 — 5000 mm
Número de especies		
criptógamas	186	95
helechos arbóreos	12	6
helechos herbáceos	26	16
helechos epifíticos	28	18
musgos	75	34
hepáticas	45	21

Tabla 11

Distribución altitudinal de algunas especies de musgos en áreas serpentinadas y non-serpentinadas de Cuba respectivamente (según BORHIDI y PÓCS, 1985)

	áreas non-serpentinadas Sierra Maestra	áreas serpentinadas Sierra de Moa
<i>Acroporium pungens</i>	1000 — 1900 m	300 — 470 m
<i>Campylopus porphyrodietion</i>	1800 — 1950 m	600 — 800 m
<i>C. saxatilis</i>	1500 — 1800 m	200 — 470 m
<i>Isopterygium micans</i>	1500 — 1800 m	500 — 800 m
<i>Leucobryum giganteum</i>	1000 — 1800 m	600 — 900 m
<i>L. polakowskyi</i>	1100 — 1950 m	600 — 800 m
<i>Mittenothamnium reptans</i>	1200 — 1950 m	700 — 800 m
<i>Philonotis sphaericarpa</i>	1600 — 1900 m	600 — 800 m
<i>Pogonatum tortile</i>	1000 — 1200 m	400 — 600 m
<i>Schlotheimia torquata</i>	1500 — 1800 m	200 — 800 m
<i>Syrrhopodon tenuifolius</i>	1700 — 1950 m	500 — 700 m

Por otra parte, áreas serpentinadas antiguas son capaces de conservar elementos relictos de distribución extremadamente disyunta de épocas geológicas muy tempranas. En Cuba, las siguientes especies de hepáticas pueden

considerarse como relictos de serpentina: *Calypogeia venezuelana*, *Plagiochila steyermarkii*, *Syrrophodon elongatus* (REYES, 1982).

Ya antes mencionamos una particularidad fitogeográfica importante de la serpentinita, que es el descenso de las zonas montañosas de la vegetación y de las especies montañosas y subalpinas a niveles altitudinales más bajas. Este fenómeno se manifiesta por la distribución altitudinal de una cantidad de musgos. La tabla 11 muestra la distribución altitudinal de algunas especies de musgos en distintas montañas serpentinas y non-serpentinas respectivamente. 11 especies de musgos seleccionadas están listadas que ocurren en las montañas serpentinosas en altitudes mucho más bajas que en las montañas non-serpentinosas. PÓCS explica este fenómeno (in BORHIDI et PÓCS, 1985) por el hecho que sobre serpentina las pluvisilvas montañas húmedas se desarrollan solo en los valles profundos, mientras los pendientes y crestas están cubiertos por bosques siempreverdes esclerófilos o bosques arbustivos más abiertos condicionados por suelos de serpentina secos y pobres en nutrientes. En las comunidades posteriormente mencionadas especies de las pluvisilvas húmedas crecen muy raramente y están reemplazadas mayormente por elementos xerófitos. Mucho de ellos son elementos de los bosques nublados y matorrales subalpinos o subpáramos de las zonas vegetales de mayor altitud, que ocurren en las zonas bajas como relictos. La tabla 12 muestra algunas especies que ocurren en los Andes y en las demás Antillas entre 2000 and 3000 metros de altura mientras en Cuba viven las mismas como relictos aislados en altura mucho más baja y exclusivamente sobre rocas de serpentinitas.

Tabla 12

Distribución altitudinal de algunas especies de briófitos en América Latina
(según PÓCS in BORHIDI et PÓCS, 1985)

	Antillas y Andes	en Cuba, sólo en serpentinitas
<i>Leskeodon andicola</i>	2000 — m	400 — 500 m
<i>Plagiochila steyermarkii</i>	2200 — m	1000 — 1100 m
<i>Drepanolejeunea suchaeta</i>	1000 — 2500 m	900 — 1100 m
<i>Leptoscyphus cuneifolius</i>	— 3000 m	800 — 1100 m
<i>Calypogeia venezuelana</i>	— 2000 m	400 — 1000 m

La vegetación esclerófila y serpentinitas

En el clima tropical, la roca serpentina favorece principalmente a la dominancia y distribución de los arbolitos y arbustos esclerófilos. Por este efecto de las serpentinitas podemos explicar el hecho, de que el 46% de la flora endémica de Cuba este compuesta por micro- y nanofanerófitos. El papel, que juegan las ciperáceas y gramíneas en la vegetación serpentínicola es mucho menos notable, que el desempeñado por ellos en la zona templada. Su presencia es una característica importante del estrato herbáceo de los pinares, aunque raramente es más importante en los claros de los matorrales. Por lo general, los extremos del clima tropical estacional y la compactación de los suelos favorecen su distribución, sin embargo, las gramíneas, en condiciones tropicales, se convierten en elementos dominantes solo cuando están apoyadas por influencias antrópicas.

Xeromorfismo como el síndrome adaptivo general de la vegetación

Tanto de acuerdo a nuestras observaciones ya mencionadas como a las numerosas afirmaciones contradictorias con respecto a la xeromorfía, hemos llegado a la conclusión siguiente: a pesar de que la xeromorfía de las plantas y de la vegetación se atribuye a razones ecológicas y fisiológicas extraordinariamente heterogéneas, esta se puede interpretar en forma unilateral.

La xeromorfía debe considerarse como un complejo de síntomas de adaptación — como un síndrome adaptivo general, como un cierto tipo del mecanismo de respuesta al stress — que se forma como consecuencia de una adaptación a los choques y tensiones ecológicos, causados por la falta de distintos factores necesarios; esto se fija genética- y morfológicamente en los organismos de las plantas y se manifiesta en la fisionomía de la flora y vegetación como un síndrome ecológico homogéneo. VALES expresó que en las plantas serpentínícolas las características morfológicas exteriores de xeromorfía no están correlacionadas completamente con las características anatómicas interiores provocadas por los habitats secos. En muchos casos (*Myrica shaferei*, *Bucida ophiticola*, *Neomazaea phialanthoides*) la estructura de los tejidos y los elementos del sistema vasoductorio muestran una combinación de características anatómicas xeromórficas y mesomórficas. Por esto, este tipo de la adaptación experimentado en las plantas serpentínícolas fue nominado "seudoxeromorfismo" (VALES et al. 1982, VALES et CARRERAS 1987). En algunos casos el carácter xeromórfico de la vegetación

de serpentina no refleja la sequía verdaderamente existente en la habitat, sino es una manifestación de la deficiencia del suelo en nutrientes y en micro-elementos indispensables, etc. Por esto, la xeromorfía de la vegetación de la serpentina puede ser considerada como "peinomorfía", que es la respuesta de las plantas general al stress de hambre provocado por la habitat, en nivel de la vegetación.

REFERENCIAS

- Alain, H. Liogier (1955): El endemismo en la flora de Cuba. Mem. Soc. Hist. Nat. Cubana 21/2: 187-193.
- Alain, H. Liogier (1958): La flora de Cuba: sus principales características, su origen probable. Rev. Soc. Bot. Cubana 15/2-3: 36-59.
- Antonovich, J., Bradshaw, A.D., Turner, R.G. (1971): Heavy metal tolerance in plants. Adv. Ecol. Res. 7: 1-85.
- Ascanio, O., Perez, J.M., Hernandez, A. (1968): Mapa Genético de los Suelos de Cuba 1:1 000 000. Inst. de Suelos Acad. Cien. Cuba.
- Atlas Nacional de Cuba — La Habana (1970) 132 pp.
- Atlas De Cuba (1978): La Habana, Inst. Cub. Geodes. Cart. 143 pp.
- Aubréville, A.M. (1965): Principes d'une systématique des formations végétales tropicales. Adansonia 5: 153-196.
- Basilevich, R. y otros (1969): Basic Theoretical Problems of Biological Productivity. Ed. Nauka Akad. Leningrad.
- Bauman-Bodenheim, M.G. (1955): Über die Beziehungen der neu-kaledonischen Flora zwischen tropischen und südhemisphärischen Bedingungen. Ber. Geobot. Inst. Rübel 64-71.
- Beard, J.S. (1944): Climax vegetation in tropical America. Ecology 25: 127-158.
- Beard, J.S. (1953): The Savanna Vegetation of Northern tropical America. Ecol. Mon. 23: 149-215.
- Beckett, P.H.T. (1965): The cation exchange equilibria of calcium and magnesium. Soil. Sci. 100: 118-123.
- Bennett, H.H., Allison, R.V. (1928): The Soils of Cuba. Washington, 410 pp.
- Bennett, H.H., Allison, R.V. (1966): Los Suelos de Cuba y Algunos Suelos Nuevos de Cuba. La Habana Ed. Rev. 375 pp.
- Berazain, R.I. (1976): Estudio preliminar de la flora serpentinicola de Cuba. Ciencias ser. 10. Botánica 12: 11-26.
- Berazain, R.I. (1981): Reporte preliminar de plantas serpentínicas acumuladoras e hiperacumuladoras de algunos elementos. Rev. Jard. Bot. Nac. Cuba 2: 48-59.
- Blackshaw, G.N. (1920): Magnesite impregnated soil. S. Afric. J. Sci. 17: 171-178.

- Borhidi, A. (1974): Curso de Geobotánica; Instituto de Botánica, Academia de Ciencias. La Habana.
- Borhidi, A. (1974): Mapificamos en Cuba (en Hungaro). Gondolat Budapest, 215 pp.
- Borhidi, A. (1975): The effects of serpentine soils on tropical flora and vegetation in Cuba. XII. Intern. Bot. Congr. Leningrad. Abstracts I: 110.
- Borhidi, A. (1976): Fundamentals of Geobotany of Cuba (in Hungarian). Summary of D. Sc. Theses. Budapest 1-16.
- Borhidi, A., Herrera, R. (1977): Génesis, característica y clasificación de los ecosistemas de sabana en Cuba. Cien. Biol. Acad. Cien. Cuba 1: 115-130.
- Borhidi, A., Muñoz, O. (1980): Die Vegetationskarte von Kuba. Acta Bot. Acad. Sci. Hung. 26: 25-53.
- Borhidi, A., Muñoz, O., Del-Risco, E. (1979): Clasificación fitocenológica de la vegetación de Cuba. Acta Bot. Acad. Sci. Hung. 25: 263-301.
- Borhidi, A., Pócs, T. (1985): Effects of serpentine on the distribution of Cryptogams in Cuba. Abstr. IAB Conf. of Bryoecology, Budapest-Vác-rátót, 1985. Abstracta Bot. 9. Suppl. 1:10.
- Brooks, R.R., Lee, J., Jaffré, T. (1974): Some New Zealand and New Caledonian plant accumulators of nickel. J. Ecol. 62: 493-499.
- Cabrer-Mestre, P. (1964): Introducción al estudio de las tierras aridas en la América Latina. Agrotechn. Cuba No. 1-2.
- Cain, S.A. (1939): The Climax and its complexities. Amer. Midland. Nat. 21: 146-181.
- Capote, R., Berzain, R. (1985): Clasificación de las formaciones vegetales de Cuba. Rev. Jard. Bot. Nac. Cuba 5/2: 27-76.
- Ciferri, R. (1936): Studio geobotanico dell'Isola Hispaniola. Atti Inst. Bot. Univ. Pavia 8: 3-336.
- Clements, F.E. (1916): Plant succession: an analysis of the development of vegetation. Carnegie Inst. Wash. Publ. 242: 1-512.
- Clements, F.E., Weaver, J.E. (1936): Plant Succession and Indicators. New York. 536 pp.
- Crooke, W.M. (1956): Effect of soil reaction on uptake of nickel from a serpentine soil. Soil. Sci. 81: 269-276.
- Crooke, W.M., Inkson, R.H.E. (1955): The relationship between nickel toxicity and major nutrient level. Pl. Soil. 6: 1-15.
- Dirección nacional de Suelos y Fertilizantes INRA: (ed.) (1975): Suelos de Cuba. Tomo I: Química del Suelo. Edit. Orbe, La Habana.
- Drewmann-Reilly, C. (1972): Observation on copper-tolerance in the vegetation of a Zambian copper clearing. J. Ecol. 60: 439-444.
- Duvigneaud, P. (1959): Plantes cobaltophytes dans le Haut-Katanga. Études sur la végétation du Katanga et de ses sols métallifères, 2. Bull. Soc. Roy. Bot. Belg. 91: 111-134.
- Duvigneaud, P. (1966): Note sur la biochimie des serpentines du sud-ouest de la France. Bull. Soc. Roy. Bot. Belg. 99: 271-329.

- Duvigneaud, P., Plancke, J. (1959): Les "Acrocephalus" arborescentes des plateaux Katagais. Études sur la végétation du Katanga et de ses sols métallifères, 5. Biol. Jaarb. Gand. 27: 214-257.
- Duvigneaud, P., Timperman, J. (1959): Études sur le genre Crotalaria. Bull. Soc. Roy. Bot. Belg. 91: 135-176.
- Eiten, G. (1972): The Cerrado Vegetation of Brasil. Bot. Rev. 38: 201-341.
- Finko, V.I., Korin, I.Z., Formell, C.F. (1967): Sobre la edad de la corteza de intemperismo y las lateritas de Cuba. Rev. Geol. Acad. Cien. Cuba 1(1): 29-47.
- Furazzola-Bermudez, P.J. y otros (1964): Geología de Cuba. Cons. Nac. Cuba, La Habana; 239 pp.
- Gams, H. (1930): Über die Reliktöhrenwälder und das Dolomitphänomen. Veröff. Geobot. Inst. Rübel 6: 32-80.
- Gigon, A., Rorison, I.H. (1972): The response of some ecologically distinct plant speices to nitrate and to ammonium nitrogen. J. Ecol. 60: 93-102.
- Gregory, R.P.G., Bradshaw, A.D. (1965): Heavy metal tolerance in populations of Agrostis tenuis Sibth. and other grasses. New Phytol. 64: 131-143.
- Good, R. (1954): The Geography of the Flowering Plants. Longmans Gren and Co. London. 452 pp.
- Gordon, A., Lipman, C.B. (1926): Why are serpentine and other magnesian soils unifertile? Soil. Sci. 22: 291-302.
- Göhlert, F. (1928): Die Flora über Eisenkarbonat. Biol. Gener. (Wien) 4: 333-336.
- Hardy, F. (1940): A provisional classification of the soils of Trinidad. Trop. Agr. (Trinidad) 17: 153-158.
- Hardy, F. (1945): The soils of South America. In: Verdoorn: Plants and Science in Latin America. 2: 322-326.
- Hattori, S. (1955): Hepaticae occurring on serpentine on Mt. Apoi (Hokkaido). Bot. Mag. Tokyo 68: 320-323.
- Hernandez, A. (1966): Importancia del estudio genético de los suelos: su aplicación en la prov. de Las Villas. Tecn. Agropec. No. 2.
- Hernandez, A. y otros (1975): Génesis y clasificación de los suelos de Cuba. Acad. Cien. Cuba, Inst. de Suelos. La Habana, 315 pp.
- Hewetson, C.E. (1956): A discussion on the climax concept in relation to the tropical rain and deciduous forest. Emp. For. Rev. 35: 274-291.
- Holdridge, L.R. (1967): Life Zone Ecology. San José, 206 pp.
- Howard, A.R. (1973): The Vegetation of the Antilles, In: Graham, A. (ed.): Vegetation and Vegetational History of Northern Latin America. Elsevier Sci. Publ. Co. Amsterdam 1-38.
- Hunter, J.G., Vergnano, O. (1952): Nickel toxicity in plants. Ann. Appl. Biol. 39: 279-284.
- Ijzerman, R. (1931): Outline of the Geology and Petrology of Surinam.
- Jacobsen, W.B.G. (1967): The influence of the copper content of the soil on the vegetation at Silverside North Mangula area. Kirkia 5: 259-277.

- Jacobsen, W.B.G. (1968): The influence of the copper content of the soil on trees and shrubs at Molly South Hills, Mangula. Kirkia 6: 63-84.
- Johnson, C.M., Pearson, G.A., Stout, P.R. (1952): Molybdenum nutrition of crop plants. II. Plant and Soil 4: 178-196.
- Kitamura, S. (1950): Adaptation and isolation on the serpentine areas. Acta Phytotax. Geobot. 12: 178-185.
- Klimes-Szmik, A., Suarez Diaz, O., Mesa Nápoles, A., Peña Velez, J. (1980): Suelos de Cuba, Tomo II: Física del Suelo. Edit. Orbe, Ciudad de La Habana.
- Klinge, H. (1965): Podzol soils in the Amazon Basin. J. Soil Sci. 16: 95-103.
- Klinge, H., Rodriguez, W.A., Brunig, E., Fitthau, E.J. (1975): Biomass and Structure in a Central Amazonian Rain Forest. In: Golley, F.B., Medina, E. (eds): Tropical Ecological Systems. Ecol. Stud. 11: 115-122.
- Knapp, R. (1965): Die Vegetation von Nord- und Mittelamerika. Fischer, Stuttgart-Jena, 373 pp.
- Krause, W. (1958): Pflanzendecke und Standort auf Serpentin. Handb. d. Pflanzenphysiol. 4: 755-798.
- Krause, W. (1958b): Boden und Pflanzengesellschaften. Ibidem 807-850.
- Kruckeberg, A.R. (1954): The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology 35: 251-258.
- Lam, H.J. (1927): En plantengeografisch Dorado. Handlg. IV. Nederl. Ind. Naturw. Congr. 386-397.
- León, H. Sauget, Alain, H. Liogier (1946-1962): Flora de Cuba I-V. La Habana.
- Lyon, C.L., Peterson, P.J., Brooks, R.R., Butler, G.W. (1971): Calcium, Magnesium and trace elements in a New Zealand flora. J. Ecol. 59: 421-429.
- Marie-Victorin, H., León, H. Sauget (1942, 1944, 1956): Itinéraires botaniques dans l'île de Cuba. Contr. Inst. Bot. Univ. Montreal, No. 41. 496 pp., No. 50. 410 pp., No. 68. 227 pp.
- Mason, H.L. (1946): The edaphic factor in narrow endemisms. I. The nature of environmental influence. Madroño 8: 209-226.
- Maul, F. (1975): Introducción al conocimiento de los suelos tropicales y subtropicales (en húngaro). In: Pál, I. (ed.): Conocimientos botánicos y zoológicos de la zona caliente. Univ. Textbook, Gödöllő, 16-33.
- Minguzzi, C., Vergnano, O. (1953): Il contenuto di elementi inorganici delle piante della formazione ofiolitica dell'Impruneta. Nuovo Giorn. Bot. Ital. N.S. 60: 287-319.
- Muñiz, O. (1970): Endemismo en la flora de Cuba, In: Atlas Nac. de Cuba, p. 57, p. 60.
- Muñiz, O., Borhidi, A. (1983): Catálogo de las palmas Cubanas. Acta Bot. Acad. Sci. Hung. 28: 309-345.
- Novák, F.A. (1928): Quelques remarques relatives au probleme de la végétation sur les terrains serpentiniques. Preslia 6: 42-71.

- Novák, V., Pelisek, J. (1940): Rendzinaböden auf Serpentin gestein. Ann. Fac. Agron. Bucarest. 11.
- Nuñez-Jimenez, A. (1959): Geografia de Cuba. La Habana.
- Nuñez-Jimenez, A. (1967): Notas preliminares acerca del carso en peridotitas de la Sierra de Moa, Oriente. Rev. Geol. Acad. Cien. Cuba 1: 5-28.
- Odum, E.P. (1959): Fundamentals of Ecology. 2. ed. Saunders, New York, 546 pp.
- Proctor, J. (1970): Magnesium as a toxic element. Nature, 227: 742-743.
- Proctor, J. (1971a): The plant ecology of serpentine, II. Plant response to serpentine soils. J. Ecol. 59: 397-410.
- Proctor, J. (1971b): The plant ecology of serpentine, III. The influence of a high magnesium/calcium ratio and high nickel and chromium levels in some british and Swedish serpentine soils. J. Ecol. 59: 827-842.
- Proctor, J., Woodell, S.R.J. (1971): The plant ecology of serpentine, I. Serpentine vegetation of England and Scotland, J. Ecol. 59: 375-395.
- Raunkiaer, C. (1907): Livsformernes Statistik Som Grundlag for biologisk Plattegeographi. Bot. Tidsker.
- Richards, P.W. (1952): The Tropical Rain Forest. Cambridge, 450 pp.
- Richards, P.W. (1955). The secondary succession in the tropical rain forest. Sci. Prog. 43: 45-57.
- Robinson, W.D., Edgington, G., Byers, H. (1935): Chemical studies on infertile soils derived from rocks high in magnesium and generally high in chromium and nickel. U.S. Pept. Agricult. Techn. Bull. 471.
- Rune, H. (1953): Plant life on serpentine and related rocks in the North of Sweden. Acta Phytogeogr. Succ. 36: 1-139.
- Samek, V. (1973): Regiones fitogeográficas de Cuba. Acad. Cien. Cuba, serie Forest, No. 15. 1-60.
- Sarasin, F. (1917): Neu-Caledonien un die Loyalty Inseln. Basel Georg and Co.
- Seifriz, W. (1942): The plant life of Cuba. Ecol. Mon. 13: 375-426.
- Severne, B.C., Brooks, R.R. (1972): A nickel-accumulating plant from Western Australia. Planta 103: (1): 91-94.
- Soane, B.D., Sauder, D.H. (1959): Nickel and chromium toxicity of serpentine soils in Southern Rhodesia. Soil Sci. 88: 322-329.
- Stark, N. (1970): The nutrient content of plants and soils from Brasil and Surinam. Biotropica 2: 51-60.
- Tüxen, R. (1933): Klimaxprobleme des NW-europäischer Festlandes. Ned. Kruidk. Arch. 43.
- Vales, M., Borhidi, A., Del-Risco, E. (1982): Anatomía de la madera de Myricaceae en Cuba: Consideraciones ecológicas. Acta Bot. Acad. Sci. Hung. 28: 241-253.
- Walker, R.B. (1954): Factors affecting plant growth on serpentine soils. Ecology 35: 259-266.
- Walter, H. (1970): Vegetationszonen und Klima. Fischer, Jena; 244 pp.
- Whittaker, R.H. (1954): The vegetational response to serpentine soils. Ecology 35: 275-288.

- Whittaker, R.H. (1965): Dominance and diversity in land plant communities. Science 147: 250-260.
- Wild, H. (1968): Geobotanical anomalies in Rhodesia, I. The vegetation of copper bearing soils. Kirkia 7: 1-71.
- Wild, H. (1970): Geobotanical anomalies in Rhodesia, III. The vegetation of nickel-bearing soils. Kirkia 7: (Suppl.) 1-62.
- Wiltshire, G.H. (1972): Growth of plants on soils from two metalliferous sites in Rhodesia. J. Ecol. 62: 501-525.
- Wiltshire, G.H. (1972): Effect of nitrogen source on translocation of nickel in some crop plants and weeds. Kirkia 8: 103-123.
- Zonn, S.V. (1968): Osobennosti pochvoobrasovaniya i glavniya tipi pochv Kubi. Genet. Geogr. Pchv. Dokl. IX. Meshdunarodn. Kongr. Pchvoved. Moskow. 53-152.
- Zonn, S.V., Vazquez, L.R., Cabrer-Mestre, P. (1966): Opit postreneniya geneticheskoy klassifikacii pochv Kubi. Pochvovedeniye, No. 12.
- Zólyomi, B. (1942): A Középdunai flóráválasztó és a dolomitjelenség. — Die Mittel-Donau Florenscheide und das Dolomitphänomen. Bot. Közlem. 39: 209-224.

DISPERSAL AND GROWTH-FORMS: AN APPROACH TOWARDS AN UNDERSTANDING OF THE
LIFE-STRATEGY CONCEPT IN LICHENOLOGY

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Dispersal mechanisms, successions and growth-rates of epiphytic lichen populations were investigated in differently polluted regions of West-Hungary. Effects of SO_2 , NH_4^+ and bark-pH were taken into consideration as ecological factors, influencing the dynamical behaviour of lichen populations. Apart from dynamical characteristics, the growth-form served as statical attributum. The joint application of these attributes served the idea of life-strategy concept in lichenology.

Results showed that dispersal with the aid of soredia becomes ever more important during the process of succession in all kinds of polluted regions. Lecanora conizaeoides and Lepraria incana showed high tolerance against the acidification of the bark caused by rain or melting snow. In the SO_2 polluted areas dispersal by thallus fragments has crucial importance, because the production of soredia, isidia or spores is highly limited. The development of Parmelia caperata synsium were observable only in the non-polluted regions within Castanetum sativae noricum associations. In orchards small foliose, ruptured foliose or fruticose colonies were dominated on the trees. The atmospheric NH_4^+ facilitated the growth-rates of epiphytic lichen populations, except the species of Parmelia exasperatula.

Results showed the advantage of the application of the life-strategy concept because it makes possible to earn many-sided informations about different kinds of environmental quality. Modifications, morphological performances, changes in dispersal capacities together give us suitable informations about the responses of cryptogamic populations to ecological influences.

INTRODUCTION

Dispersal — in its broadest sense — embraces types of dispersing propagules, dispersal mechanisms, attachment and its supporting and limiting factors as well (BAILEY 1976).

The anatomy and morphology of dispersing propagules is well known (ACHARIUS 1810, SCHWENDENER 1860, BITTER 1901, Du RIETZ 1924, BARKMAN 1958,

PYATT 1974, JAHNS 1974, POELT 1974), and LETROUIT-GALINOU (1966, 1968, 1970, 1974 etc.) who has investigated the anatomical and histological structure of generative organs in considerable detail.

The first review study concerning dispersal, attachment and establishment of different kinds of propagules was undertaken by BAILEY (1976) based mainly on results of his own researches (e.g. BAILEY 1966a, b, 1968a, b, 1970).

Propagules can be divided into two main groups, namely asexual and sexual: asexual propagules are vegetative diaspores (soredia, isidia, conidia) and in some cases fragments of thalli: sexual ones are spores produced in different kinds of ascocarps. Propagules dispersed by either active or passive mechanisms. In the passive distribution of the propagules wind and water are very important factors but animals also play an important role (BARKMAN 1958, COKER 1967, GERSON 1973, KISS 1984). Propagules dispersed by horizontal movements of air, as well as thermal micro-currents (convection) developed along bark surfaces heated by sun.

Du RIETZ (1924) observed soredia and thallus fragments in snow falls. He concluded that the abundance of airborne propagules of lichen taxa are more or less proportional to the abundance of the lichen species concerned. Spores of Buellia sp. were trapped by RUDOLPH (1970) in the air of Antarctica. Spores are light and actively discharged to small distances from the ascocarps. This is one of the main types of dispersal for crustose species: dispersal by thallus fragments is very rare in this type of growth-form except in polluted areas. Although a high quantity of spores is produced by such species they are unfortunately without their algal symbiont partner.

Isidia, soredia and thallus fragments are important in the case of foliose, threadlike, fruticose and Cladonia growth-forms. Although dispersal by these kinds of propagules is somewhat clumsy or difficult — for example BAILEY (1976) has written: "... dispersal of soredia from Evernia prunastri and Ramalina farinacea is effective only up to 30 m and 20 m respectively from the source..." — these vegetative diaspores contain the whole symbiosis.

BRODIE and GREGORY (1953) and BAILEY (1966a) have investigated wind liberation of the soredia from dry and wet surfaces. BAILEY (1966a) has researched the liberation of soredia by wind from Lecanora conizaeoides, Hypogymnia physodes and Pertusaria amara, and the removal of small thallus fragments from Cladonia impexa (C. portentosa).

In a laboratory experiment approximately 2.2 m diameter rainwater

droplets were simulated to fall on thalli with 650 cm s^{-1} terminal velocity. It was found that the wet thalli of Lecanora conizaeoides liberated more soredia than dry ones in a ratio of 5:2. The reverse situation was found in the case of Hypogymnia physodes, where a ratio of c. 8 dry : 1 wet was observed. Soredia were water-dispersed from the surface of L. conizaeoides up to a distance of 61 cm.

NEW RESULTS

The spread of L. conizaeoides in West Hungary, especially in the Szombathely region is being investigated in some detail (KISS-SEAWARD 1984, KISS 1984). Downward extension is a very important and rapid process in the spread of leprose taxa such as Lepraria incana, but the soredia of L. conizaeoides are also transported by rainwater along rain-tracks. This phenomenon is observable on Fig. 1., where the pattern shows an important extension of L. conizaeoides between 1984 and 1985. The thalli of these species were not observed prior to 1984 at this site.

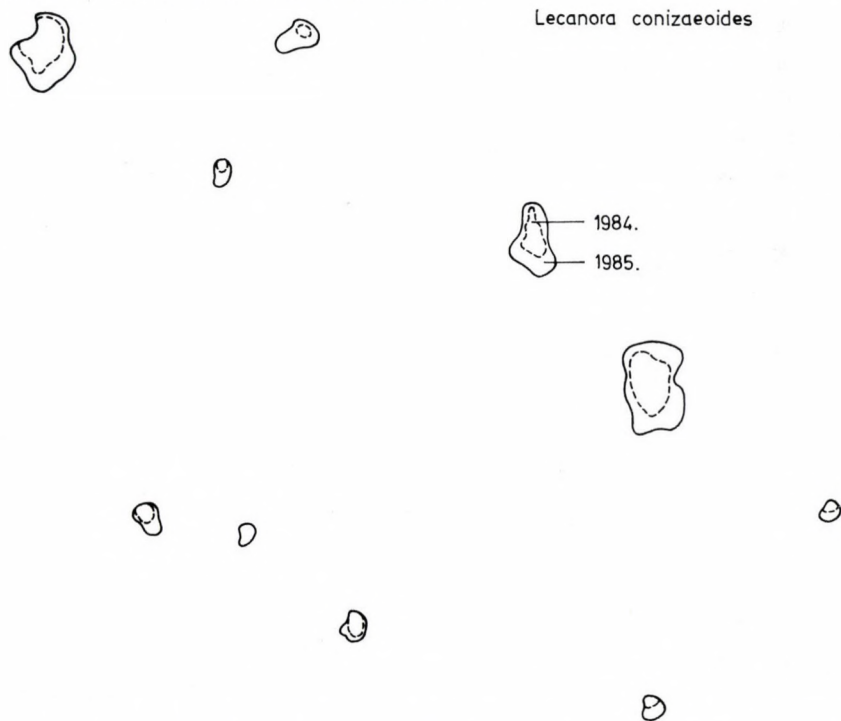


Fig. 1. Colonies of Lecanora conizaeoides on a 50 year-old Tilia cordata in Szombathely

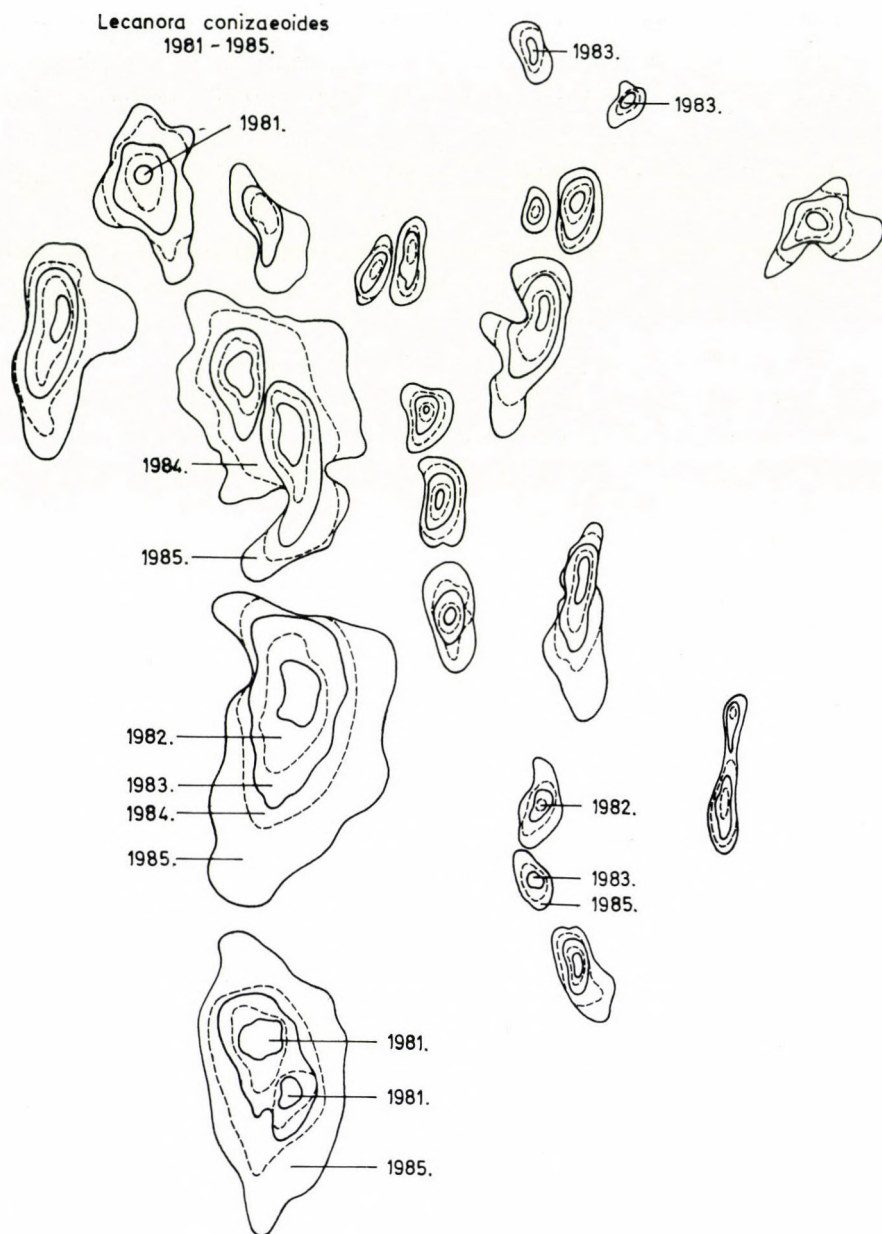


Fig. 2. Downwards extension of thalli of *Lecanora conizaeoides* between 1981 and 1985. Many small thalli have been merged into greater aggregates

Figure 2 is derived from a study of an old Betula pendula, in Gayer park in Szombathely. An intensive dispersion of thalli of L. conizaeoides has been observed over the past 5 years (1981-85). The downward extension was facilitated by large quantities of melting snow which fall during the winter of 1984/85. The acidification of the snow appeared to have no harmful effect on the thalli of this species.

Figure 3 shows a characteristic pattern of a north-facing bark surface of an 80 year-old Tilia cordata ("Park Jókai") in Szombathely. Lepraria

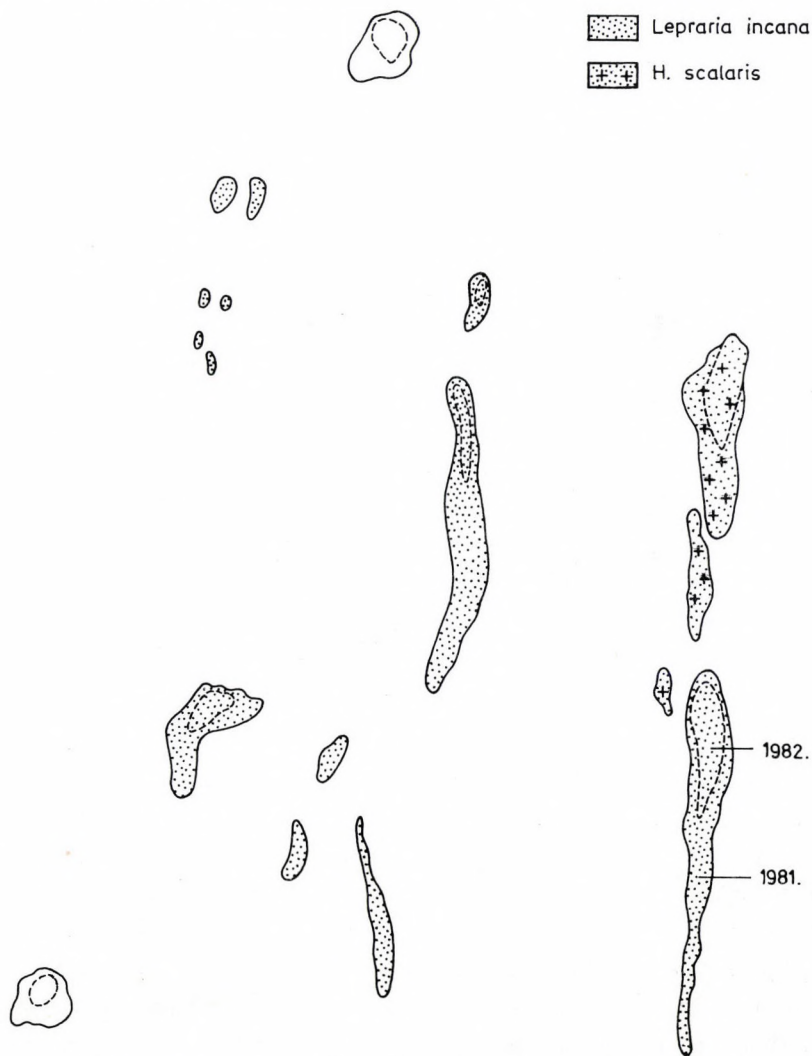


Fig. 3. A characteristic pattern of lichen thalli from a 80 year-old Tilia cordata



Evernia prunastri



1982.



Hypogymnia physodes

Fig. 4. Crustose, foliose and smaller, compact fruticose thalli on a 80 year-old Tilia cordata tree in the park region of Szombathely city

incaca as a sorediate-leprose species occurs usually in the rain-tracks. The small foliose and sorediate thalli of Hypocenomyce scalaris are also well dispersed along rain-tracks. The rain drops have an important role dispersing these taxa. Leprose, crustose and small foliose sorediate colonies are able to establish themselves in polluted areas since they have both tolerance to air pollution and effective dispersing capacities.

Figure 4 has been produced from data derived from a permanent quadrat on a north-facing surface of an 80-year old Tilia cordata between 1979 and 1984. The fruticose Evernia prunastri and the foliose Hypogymnia physodes showed no growth between 1979 and 1984. Lecanora conizaeoides was

detectable first in 1982: its colonies showed "enormous" growth and spread in this quadrat after this date.

Discharge is initiated by moistening the ascocarps (SCOTT 1959). However according to BAILEY (1976) "... opinions vary as to whether discharge occurs as a result of drying and consequent rupturing of the asci or continually while the asci are moist". PYATT (1974) has pointed out that discharge occurs always under stress, whether by loss of water when drying or absorption of water while moist.

The seasonality of spore production is also an important aspect in the study of dispersal dynamics. According to DES ABBAYES (1951), spore production in Western Europe is most active during the spring. VERSEGHY (1965) has pointed out that in dry years spore production was most intensive in spring, and in wet years was also intensive in autumn. PYATT (1969) concluded that the most intensive period of spore production is between September and February. PYATT (1979) also investigated the rate of the germination of ejected spores 7 days after discharge. The number of discharged spores in an experimental sample of Lecanora conizaeoides was between 200 and 1000 in July, in August and in September with a peak in October (of over a thousand). The germination of spores was only observed in December, but the germination in cold seasons could be of great advantage for one species over other ones. In the same experiment PYATT also showed there was a massive spore discharge by Xanthoria parietina between October and February with over 1000 spores liberated per month. Germination was in October only. Naturally spore production could change according to different micro-sites, e.g. in different microreliefs of barks.

The acidity of water — for example rainwater — also has a great influence on the spore production. PYATT (1968a, 1969, 1974) demonstrated that the optimal pH values for such in Xanthoria parietina are between 4 and 5, and for Graphis elegans between 5 and 6.

Bark pH investigations were carried out in the park region of Szombathely from September to the end of December in 1983. The sulphur dioxide pollution in this region could be as high as $150 \mu\text{g m}^{-3}$ in wintertime. Small dead surface flakes of bark were removed from 80 year-old Tilia cordata together with L. conizaeoides and Lepraria incana where these taxa were predominant. At the same time bark flakes were collected from those trees where these species were absent.

Six trees were marked for investigation and the pH values of 10 samples were measured in each month from each tree. The bark material was

crushed and 2 g from it was soaked for 2 hours in distilled water. Measurements were carried out using a Radelkis 205 Precision pH Metre with combined glass-electrode. On the basis of 240 measurements, the results were as follows:

Taxa and bark	\bar{x}	s
Pure bark	4.10	± 0.25
Bark + <i>L. conizaeoides</i>	4.65	± 0.30
Bark + <i>Lepraria incana</i>	4.80	± 0.08

\bar{X} = mean, s = standard deviation

The s values show clearly that *Lecanora conizaeoides* can tolerate not only low pH values — for instance 2.8–3.0 — but greater fluctuations than *Lepraria incana*. This is also an advantage over other populations competing for resources or space.

PYATT (1974) provided interesting data on the relationship between spore germination and air pollution. PYATT (1969a) calculated that the average germination of ascospores of *Lecidea macrocarpa*, collected near a pollution source (Port Talbot), was 62% after 14 days in a humid atmosphere. The germination of the spores was 79% when collected from a more distant from the pollution source. It is well known that polluted air may kill propagules or inhibit their germination (BAILEY 1976, KOFLER et al., 1969).

PYATT (1974) observed that "... aggregation of spores may give spores in groups a degree of protection against certain environmental conditions. This can be shown by collecting spore deposits of *Lecanora conizaeoides* and *L. subfusca* on microscope slides. As slides dried the spores moved distance of up to 80 μ m until large groups of ascospores were obtained. When these slides were placed in a humid atmosphere the spores separated".

KOFLER et al. (1969) studied the effects of dust upon spore germination. They concluded that dust from calcium carbide and iron alloy factories strongly inhibited germination of the spores of *Physconia pulverulenta*. Further work showed that *Lecanora dispersa* and *Xanthoria parietina* were much more resistant. AM ENDE (1950) has pointed out that bark extract and compounds like erythritol, glycerol and pectin accelerated germination of spores of *Xanthoria parietina*. SEAWARD (1976) investigated the reproductive behaviour of thalli of *Lecanora muralis* in material transplanted into pol-

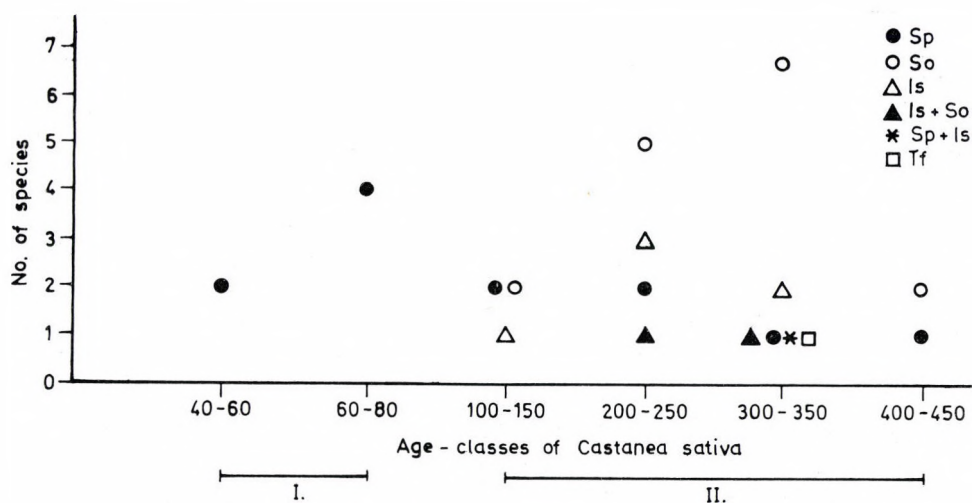


Fig. 5. Lichen succession on Castanea sativa trees in non-polluted area and the changes of the dissemination spectra according to the age-classes of the trees. Key: Sp = dispersing by spores, So = dispersing by soredia, Is = dispersing by isidia, Is + So = dispersing by isidia and soredia, Sp + Is = dispersing by spores and isidia, Tf = dispersing by thallus fragments

luted areas, and demonstrated swelling and eruption, and finally total disappearance of the central area of the thallus.

The production and the dispersal of generative and vegetative propagules are under the control of external climatic and pollution factors. These factors are in a permanent dynamic contact with the internal tolerance limits of the colonies or species.

LAUNDON (1967) observed that lichen communities are able to maintain themselves at certain levels of air pollution but they are unable to establish themselves afresh. The present author has drawn similar conclusions on the basis of his investigations on the relationships between the dispersal spectrum and lichen succession in polluted and in non-polluted areas (KISS 1983, 1985). Examinations were carried out on the boles of Castanea sativa and Juglans regia using 400 cm² and in the case of older



Fig. 6. Lichen succession on Castanea sativa bark in polluted area

trees 800 cm² quadrats between 1979 and 1984. Figure 5 shows the two main stages of the lichen succession according to the age-classes of Castanea sativa trees in the Castanetum sativae noricum (Soó) association. In West Hungary with a temperate mild-subatlantic climate (average precipitation 800–900 mm yr⁻¹) Castanea sativa forms woods usually with southern exposure at an altitude of 400 m above s.l. In these sunny woods the epiphytic lichen vegetation is well developed.

We can follow the succession on the basis of Fig. 5. Six dispersal types are distinguishable on the boles. The richest lichen vegetation was observed on the 200 to 300 year old boles with bark pH values of 5 and 6. Dispersal with the aid of soredia increases with the succession and becomes more predominant on the 100–150 year old boles.

At the same tree, in a polluted area where in the wintertime SO₂ concentration reaches 150 µg m⁻³, the succession and the dispersal show a quite different picture: Fig. 6 has been prepared from an orchard found between Szombathely city and Olad village, where Castanea sativa had been planted 300 and 400 years ago. The majority of the fruit trees are pears and apples, which are sprayed once or twice a year. The pH values of the bark are much lower, usually between 4 and 5, than in the Castanetum sativae associations. Here we can distinguish only three types of dispersal, the most important being sorediate, but dispersal with the aid of thallus fragments is ever more important.

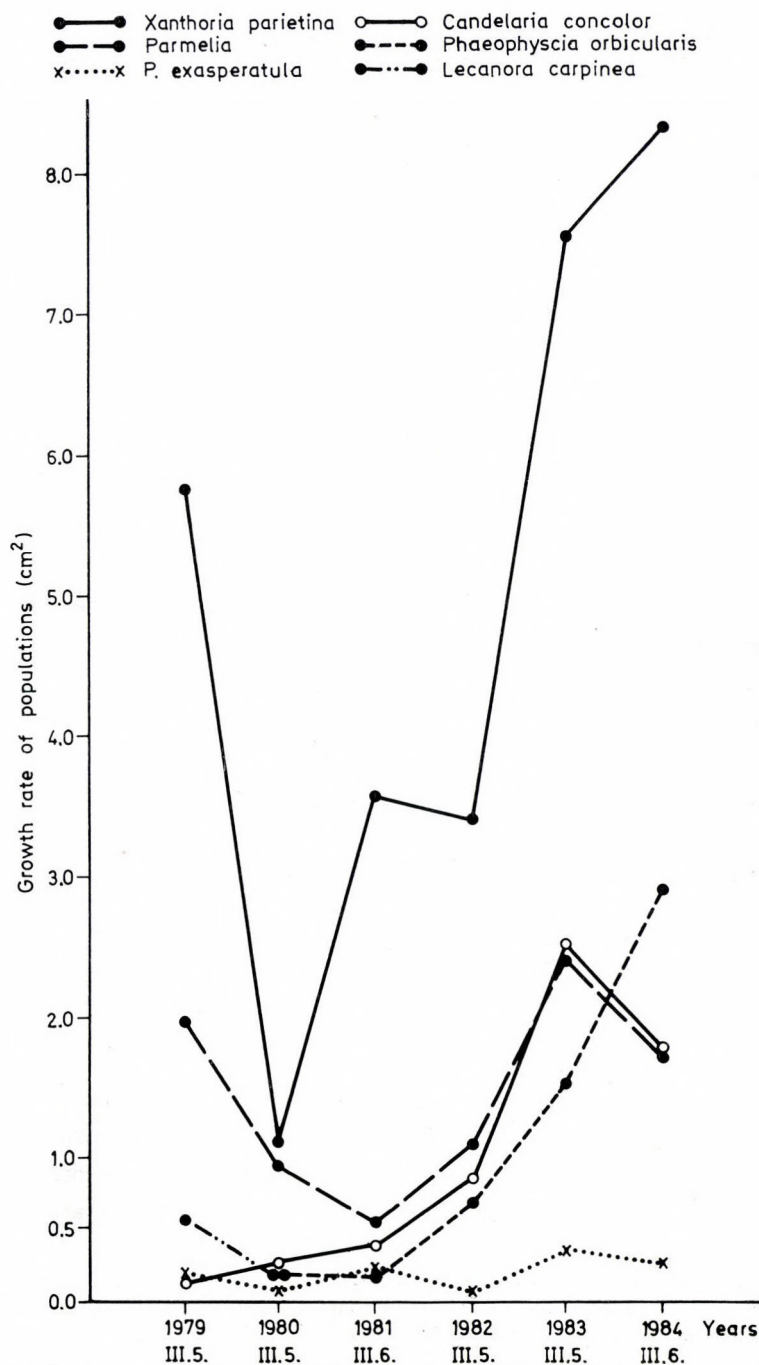


Fig. 7. Growth rate curves of lichen populations living around farm buildings in Magyarszombatfa village

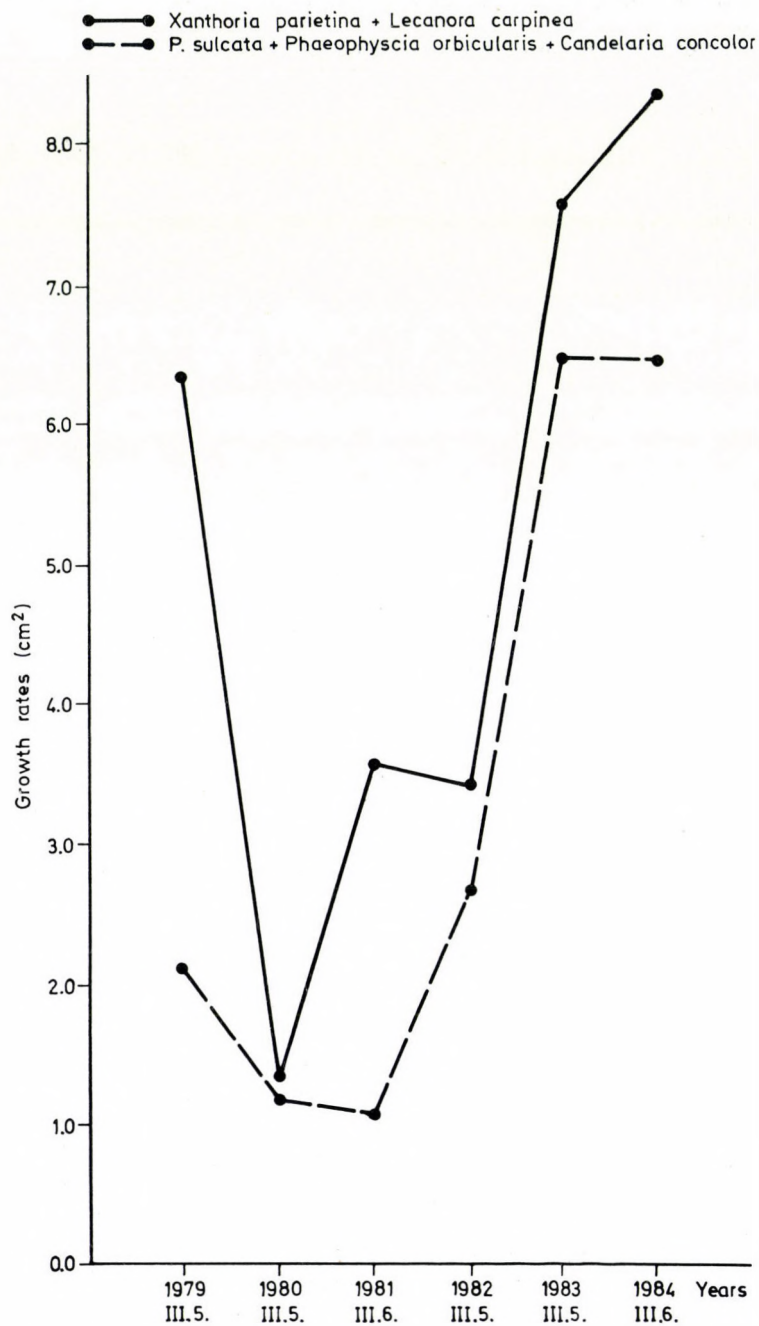


Fig. 8. The summed growth rates of populations including the same type of dispersal

The whole development of Parmelia caperata synusium is impossible in this polluted area, only a few small thalli being present. Thalli of Hypogymnia physodes and Parmelia sulcata are without soredia and those of Parmelia tiliacea are without isidia. In this area only the small foliose colonies, such as Physcia adscendens, P. tenella and Gandelaria concolor, were able to produce soredia.

In the next example we see a characteristic transitional state of the epiphytic lichen succession, between the crustose and foliose ones. Locality: Magyarszombatfa village, around farm buildings on the northern face of a 50 year old Juglans regia tree, at a height of 1 m. Sewage sludge is usually drained on the surface of the soil, so the NH_4^+ is a very important factor in the air at these sites. The interpretation of the trend of the dissemination or dispersal spectrum and the succession can be expressed here on the basis of the growth rate of the populations determined between 1979 and 1984.

Figure 7 shows the growth rate of the populations without any attention to the dispersal types. It can be clearly observed that the thalli of Lecanora carpinea were overgrown by foliose colonies up to 1980 (KISS 1982). It seems that Xanthoria parietina has been the predominant species since that data. The exponential growth of the population of Phaeophyscia orbicularis is also conspicuous. The graphical curve of Candelaria concolor and Parmelia sulcata show similar shape up to 1983 otherwise they are typical sigmoid ones. This habitat is not suitable for the growth of the isidiate Parmelia exasperatula.

Figure 8 shows on the other hand the growth rate of the populations spreading by spores for L. carpinea, X. parietina is hardly increased. On the contrary, the colonies are spreading via soredia show an enormous growth and spread over the bark. During the latter phase of the succession on the older trees, with the senescence and degeneration of the larger foliose thalli, a small foliose layer will developed, dominated by Phaeophyscia orbicularis.

This is a characteristic assemblage of the village area of West Hungary, especially on Juglans regia boles. However, there are some exceptions to this sequence when the first colonizer, instead of the crustose species is the small foliose Phaeophyscia orbicularis. In such cases thalli of Xanthoria parietina will colonize the surface of the thalli of Phaeophyscia orbicularis or fill the gaps between the colonies together with other small foliose taxa such as Candelaria concolor and Physcia tenella.

These successional trends have also been observed in rural areas of North-Eastern Poland in 1984.

CLOSING WORDS

The main purpose of this study was to give a short review about the results and problems of lichen ecological researches in dynamical point of view.

Researches about growth- or life-forms and dissemination types of lichen species and lichen communities were the first steps toward the development of life-strategy concept.

Lichens and bryophytes have been often classified according to their life- or growth-forms (BARKMAN 1958, MÄGDEFRAU 1969, MATTICK 1950). These classifications are dated back to the physiognomical concept of HUMBOLDT (1806) and the life-form system of RAUNKIAER (1904, 1937). The growth-forms referred to morphological, the life-forms first of all the physiological characters of the thalli (e.g. BARKMAN 1958).

However the rigid separation of life- and growth-form didn't take into consideration the fact that, in the case of poikilohydric organisms, there are very close relationships between the morphology and physiology induced by environmental fluctuations (SMITH 1979, KISS 1985).

"The life-strategy refers primarily to the life history traits..." including the growth and life-form conceptions, too (JOENJE and DURING 1977, DURING 1976, ORBÁN 1984). GAMS (1932, in VERDOORN) has already written about these as "ecological units" and remarked: "Life-forms can be classified either morphologically or ecologically". His ideas and his system (1918) were one of the most important basis of the life-strategy concept. The above mentioned results and GALLÉ's explanation (1976-77) also showed that the some of the poikilohydric organisms are in a very intimate contact with the environment. For this reason there are lot of so-called "environmentally induced modifications" (POELT 1974) in lichens. WEBER (1977) has written: "Environmental modification in the production of responses that are non-transmissible — in other words, acquired characteristics. Growth, survival and reproduction of plants occur inside a wide range of acceptable, tolerable or non-lethal environmental parameters. Towards the extremes of these ranges, plants arise visibly abnormal and their morphology may evoke questions as to their taxonomic identity".

These well observable phenomena and theoretical aspects served the

basic ideas of the elaboration of the life-strategy system of lichens (KISS 1985). Modifications, morphological and histological performances, dispersal capacity or reproductive behaviour and growth rate together give us suitable informations about the responses of lichen populations to environmental stresses.

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I'm grateful to Dr. M.R.D. SEAWARD for many fruitful personal discussion about this topic at Bradford University in 1985 and for many interesting reprints.

REFERENCES

- Abbayes, H. des (1951): Traité de Lichenologie. Paul Lechevalier, Paris.
- Acharius, E. (1810): Lichenographia Universalis. Gottingiae.
- Am Ende, J. (1950): Zur Ernährungsphysiologie des Pilzes der Xanthoria parietina. Arch. Microbiol. 15: 185-202.
- Barkman, J.J. (1958): Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum, Assen.
- Bailey, R.H. (1966a): Studies on the dispersal of lichen soredia. J. Linn. Soc. Bot. 59: 479-490.
- Bailey, R.H. (1966b): Notes upon the germination of lichen ascospores. Revue Bryol. et Lichénol. 34: 852-853.
- Bailey, R.H. (1968a): Dispersal of lichen soredia in water trickles. Revue Bryol. et Lichénol. 36: 314-315.
- Bailey, R.H. (1968b): Lecanora conizaeoides in Iceland. Lichenologist 4: 73.
- Bailey, R.H. (1970): Animals and the dispersal of soredia from L. conizaeoides Nyl. ex Crombie. Lichenologist 4: 256.
- Bailey, R.H. (1976): Ecological Aspects of Dispersal and Establishment in Lichens. In: "Lichenology: Progress and Problems." Eds: D.H. Brown, D.L. Hawksworth and R.H. Bailey. pp. 215-247. Academic Press, London and New York.
- Bitter, G. (1901): Zur Morphologie und Systematik von Parmelia, Untergattung Hypogymnia. Hedwigia 40. Dresden.
- Brodie, H.J., Gregory, P.H. (1953): The action of wind in the dispersal of spores from cup-shaped plant structures. Can. Journ. Bot. 31: 402-410.
- Coker, P.D. (1967): Damage to lichens by gastropodes. Lichenologist 3: 428-429.
- Du Rietz, G.E. (1924): Die Soredien und Isidien der Flechten. Svensk Bot. Tidskr. 18: 371-396.

- Du Rietz, G.E. (1931): Studier över vinddriften på snöfalt i de skandinaviska fjällen. Bot. Notiser 31: 46.
- During, J.H. (1979): Life strategies of Bryophytes: a preliminary review. Lindbergia 5: 2-18.
- Gallé, L. (1976-77): The lichen communities of Hungary. (In Hungarian.) F. Múz. Évk. 429-493.
- Gerson, U. (1973): Lichen-arthropod associations. Lichenologist 5: 434-443.
- Jahns, H.M. (1974): Anatomy, Morphology and Development. In: The Lichens. Eds: V. Ahmadjian and M.E. Hale. pp. 3-57. Academic Press, New York and San Francisco, London.
- Joenje, W. and During, H.J. (1977): Colonization of a desalinating Wadden-polder by bryophytes. Vegetation 35: 177-185.
- Kiss, T. (1982): Aspects and types of competition between lichen species in epiphytic communities. Acta Bot. Acad. Sci. Hung. 28: 113-126.
- Kiss, T. (1983): Lichen succession on Castanea sativa Mill. boles. Bot. Közlem. 70: 71-82.
- Kiss, T. (1984): The distribution of L. conizaeoides in West Hungary. Lecture on the "SEcond Conf. of Nat. Of West Hungar". In press.
- Kiss, T. (1985): The changes of dissemination spectra during the epiphytic lichen succession. Bot. Közlem. 72: 169-180.
- Kiss, T. (1985). The life-strategy system of lichens - A proposal. Abstracta Bot. 9: 59-66.
- Kiss, T. (1985, 1987): Regressive Succession induced by acid rain in cryptogamic communities inhabiting Juglans bark. Proceedings of the IAB Conf. of Bryoecology, Budapest-Vácrátót, pp. 865-882.
- Kofler, L., Jacquard, F., Martin, J.F. (1969): Influence des fumées d'usines sur la germination des spores de certains lichens. Bull. Soc. bot. Fr., Mém. 1968 Coll. Lich. 219-230.
- Laudon, J.R. (1967): A study of the lichen flora of London. Lichenologist 3: 277-327.
- Letrouit-Galinou, M.A. (1966): Recherches sur l'ontogénie et l'anatomie comparées des apothécies de quelques Discolichens. Revue Bryol. Lichénol. 34: 413-588.
- Letrouit-Galinou, M.A. (1968): The apothecia of the Discolichenes. Bryologist 71: 297-327.
- Letrouit-Galinou, M.A. (1970): Les apothécies et les asques du Parmelia conspersa (Discolichen, Parmeliaceae). Bryologist 73: 39-58.
- Letrouit-Galinou, M.A. (1984): Sexual Reproduction. In: The Lichens. Eds: V. Ahmadjian and M.E. Hale. pp. 59-87. Acad. Press New York, London, San Francisco.
- Mattick, F. (1951): Wuchs- und Lebensformen, Bestands und Gesellschaftsbildung der Flechten. Bot. Jahrb. 75: 378-424.
- Magdefrau, K. (1969): Die Lebensformen der Laubmose. Vegetatio 16: 285-297.
- Orbán, S. (1984): A magyarországi mohák stratégiái és T, W, R, értékei. The T, W, R values and strategies of the Hungarian bryophytes. (In Hungarian). Acta Acad. Ped. Agriensis 17: 755-765.

- Orbán, S. (1984): Life strategies of Hungarian mosses and their correlation to the ecological and coenological characteristics of the environment. (In Hungarian). Thesis of CSc dissertation, Eger.
- Poelt, J. (1974): Systematic Evaluation of Morphological Characters. In: The Lichens. Eds.: V. Ahmadjian and M.E. Hale. pp. 91-111. Acad. Press, New York, San Francisco, London.
- Pyatt, F.B. (1968a): The occurrence of a rotifer on the surface of apothecia of Xanthoria parietina. Lichenologist 4: 74-75.
- Pyatt, F.B. (1969): Studies on the periodicity of spore discharge and germination in lichens. Bryologist 72: 48-53.
- Pyatt, F.B. (1974): Lichen Propagules. In: The Lichens. Eds: V. Ahmadjian and M.E. Hale. pp. 117-143. Acad. Press, New York, San Francisco, London.
- Raunkiaer, C. (1937): Plant Life Forms. Oxford.
- Rudolph, E.D. (1970): Local dissemination of plant propagules in Antarctica. In: Antarctic Ecology. Ed.: M.W. Holdgate, 2: 812-817. Acad. Press, London and New York.
- Schwendener, S. (1860): Untersuchungen über den Flechtenthallus I. Nagelis. Beitr. z. Wiss. Bot. 2. Leipzig.
- Scott, G.D. (1959): Observations on spore discharge and germination in Peltigera praetextata (Flk.) Vain. Lichenologist 1: 109-111.
- Seaward, M.R.D. (1976): Performance of Lecanora muralis in an urban environment. In: Lichenology: Progress and Problems. Eds: D.H. Brown, D.L. Hawksworth and R.H. Bailey. pp. 323-357. Acad. Press, London and New York.
- Smith, D.C. (1979): Is a Lichen a Good Model of Biological Interactions in Nutrient-Limited Environments? In: Strategies of Microbial Life in Extreme Environments. Ed.: M. Shilo, pp. 291-303. Berlin: Dahlem Konferenzen.
- Verdoorn, F.R. (1932): Manual of Bryology. The Hague (Martinus Nijhoff).
- Verseghy, K. (1965): Effect of dry periods on the spore production of lichens. Acta Biol. Hung. 16: 85-104.
- Weber, W.A. (1977): Environmental Modification and Lichen Taxonomy. In: Lichen Ecology. Ed.: M.R.D. Seaward. 9-29. Acad. Press, New York and London.

FURTHER SIX SPECIES OF USTILAGINALES, NEW TO HUNGARY

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The following six species of Ustilaginales are reported for the first time from Hungary: Entyloma polysporum on Ambrosia artemisiifolia, E. dactylidis on Deschampsia caespitosa, Tolyposporium junci on Juncus bufonius, Urocystis luzulae on Luzula luzuloides, U. beckmanniae on Beckmannia eruciformis, and Ustacystis waldsteiniae on Waldsteinia geoides. Of these Entyloma polysporum is new to Europe, and Ustacystis waldsteiniae is recorded for the second time from Europe. Luzula luzuloides is a new host for Urocystis luzulae. As a consequence of the papers of MOESZ (1950), VÁNKY, GÖNCZÖL and TÓTH (1982), VÁNKY, TÓTH, GÖNCZÖL, RÉVAY and IMRE (1985), VÁNKY (1985), and IMRE (1985), the Ustilaginales of Hungary (a country possessing an area of 93 000 km²), are relatively profoundly investigated with 125 species recorded. However, the number of species present but still unreported, probably is not negligible. Continuing our investigations on the Hungarian smut fungi, we record six species new for the country: 1. Entyloma polysporum (Peck) Farlow, in leaves of Ambrosia artemisiifolia L., 2. E. dactylidis (Pass.) Cif., in leaves of Deschampsia caespitosa (L.) Beauv., 3. Tolyposporium junci (Schröter) Woronin, in flowers and stems of Juncus bufonius L., Urocystis beckmanniae Brezhnev, in leaves of Beckmannia eruciformis (L.) Host, U. luzulae (Schröter) Winter, in leaves of Luzula luzuloides (Lam.) Dandy & Wilmott, and Ustacystis waldsteiniae (Peck) Zundel, in leaves of Waldsteinia geoides Willd.

Entyloma polysporum (Peck) Farlow, s. str., 1883: 275.

Syn. Protomyces polysporus Peck, in Thümen, Mycotheca universalis No. 1813, 1881. Type on Ambrosia trifida L., USA, New-York, Albany, X. 1880, C.H. Peck, in Thümen, Mycoth. univ. 1813.

Sori in leaves (Fig. 1) forming subcircular or, when limited by the veins, angular spots, at first light yellowish-brown, later dark green or necrotic. Spores (Fig. 3) densely crowded, globose, subglobose or rounded



Fig. 1. Sori of Entyloma polysporum (Peck) Farlow in leaves of Ambrosia artemisiifolia L.

polyangularly irregular, $9.5\text{--}13.5 \times 10\text{--}14.5\text{--}(17) \mu\text{m}$ in diam, wall slightly unevenly thickened, $0.8\text{--}2\text{--}(2.5) \mu\text{m}$ wide, smooth. Anamorph absent.

This smut has been reported on different species and genera belonging to the Compositae, and the species concept is consequently becoming rather broad. SAVILE (1947) assigned all North American species of Entyloma on Compositae, with densely crowded, rather large teliospores and lacking conidia to E. polysporum. In a narrower sense, E. polysporum occurs only on Ambrosia species (Compositae — Asteroideae), and it is known from North American and Japan. Several specimens of Entyloma compositarum on Ambrosia elatior reported from U.S.A. also belong to E. polysporum (SAVILE 1947: 109). In Hungary it was collected on Ambrosia artemisiifolia L., comit. Zala, near Keszthely, alt. c. 130 m. 15. VII. 1986, leg. E., T., U. and K. VÁNKY (BP, HUV 12228). Distributed in VÁNKY, Ustilaginales exs. No. 567.

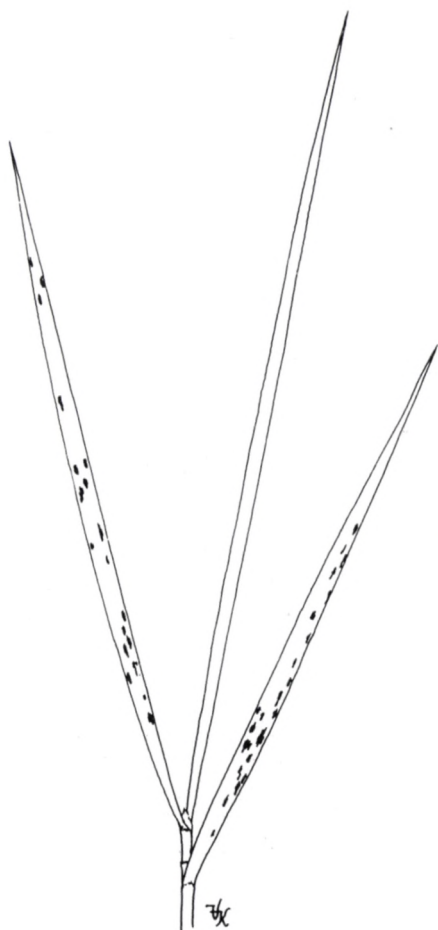


Fig. 2. Sori of *Entyloma dactylidis* (Pass.) Cif. in leaves of *Deschampsia caespitosa* (L.) Beauv.

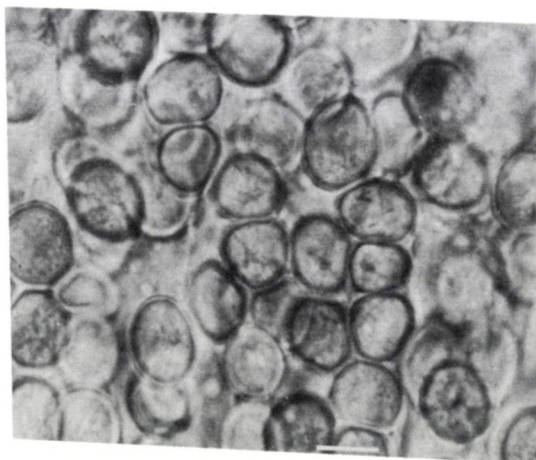


Fig. 3. Spores of *Entyloma polysporum* (Vánky, Ust. 567).
Bar = 10 μ m

Entyloma dactylidis (Passerini) Ciferri, 1924: 55

Syn. Thecaphora dactylidis Passerini, in Fischer von Waldheim, 1877: 34. Type on Dactylis glomerata L., Italy, Parma, IX, M. PASSERINI. — Entyloma crastophilum Saccardo, 1879: 540. Type on Poa annua L., Italy, Mantova, V. 1865, A. MAGNAGUTI. — Entyloma crepinianum Saccardo and Roumeguere, in Roumeguere and Saccardo, 1881: 41. Type on "Poa sudetica Haenke" (misnamed Agrostis sp.), Belgium, Malmédy, A. LIBERT, in Roumeg., Fgi. gall. exs. 1528. — Entyloma irregulare ("irregularis") Johanson, 1885: 159. Type on Poa annua L., Iceland, Eyjafjörður, Reykhús, 1883, H. STRÖMFELDT. — Entyloma catabrosae Johanson, 1885: 160. Type on Catabrosa aquatica (L.) Beauv., Iceland, Hólar, 1883, H. STRÖMFELDT. — Entyloma camusianum Hariot, 1896: 299. Type on Phleum arenarium L., France, Dépt. Loire-Inférieure, St.-Brevin, F. CAMUS. — Entyloma hieroense Hariot and Patouillard, 1904: 61. Type on Poa bulbosa L., France, Dépt. Vendée, "circa Hieroem (Noirmoutier)", CH. MÉNIER. — Entyloma sydowianum Ciferri, 1928: 20 (p. p.; nomen confusum). — Entyloma korshinskyi Lavrov, 1937: 2. Type on Hordeum disticzum L., var. nutans Schuebl. (cult.), USSR, Turkestan, near Alexeevskoje, 13. V. 1895, S. KORSHINKSY. — Entyloma camusianum Hariot var. pratense Lavrov, 1937: 2. Type on Phleum pratense L., USSR, Siberia, near Tomsk. — Entyloma alopecurivorum Lavrov, 1938: 54. Type on Alopecurus pratensis L., USSR, Siberia, Zabaikal, Ust'-Kiran, 14. VIII. 1912, P. MICHNO. — Entyloma holci Liro 1938: 97 (without Latin diagn.); 1939: 112. Type on Holcus mollis, Finland, Isthmus karelicus, Valjärvi, Veikkala, 16. VIII. 1897, G. LANG. — Entyloma deschampsiae Liro, 1938: 101 (without Latin diagn.); 1939: 112. Type on Deschampsia cespitosa (L.) Beauv., Finland, Nyland, Pornainen, 13. VII. 1915, J. I. LIRO. — Entyloma lagerheimianum Liro 1938: 102 (without Latin diagn.); 1939: 24. Type on Festuca rubra L., Sweden, Öland, Borgholm, VIII. 1908, G. LAGERHEIM (as E. ambiens), in Vgr., Microm, rar. sel. 1590. — Entyloma nubilum Liro, 1938: 102 (without Latin diagn.); 1939: 112. Type on Alopecurus pratensis L., Sweden, Uppland, Norrtälje, VIII. 1915, G. LAGERHEIM, in Lundell and Nannfeldt, Fgi. exs. suec. 1292. — Entyloma semenoviana (Lavrov) Gutner, 1941: 225. — Iolyposporella semenoviana Lavrov, 1934: 86. Type on Polypogon maritimus Willd., USSR, Kazakhstan, prov. Akmolinsk, dstr. Atbasar, near Lake Tenis, 26. VI. 1914, V.F. SEMENOV. — Entyloma polypogonis Viennot-Bourgin, 1937: 122. Type on Polypogon maritimus Willd., Portugal, Madeira Islands, in the marshes of island Deserta Grande.

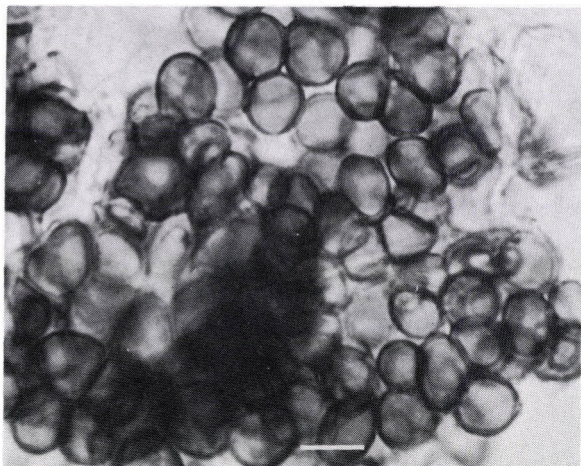


Fig. 4. Spores of Entyloma dactylidis (HUV 11355).
Bar = 10 μ m

Sori (Fig. 2) in leaves and sheaths appearing as short, linear to ovate, lead-coloured or black 0.1–2(–3) mm long, scattered to sometimes confluent, often moderately swollen spots. Spores (Fig. 4) densely packed, tending to adhere in irregular groups, variable in form and size, from globose to irregularly polyangular, 5–11 \times 6–15(–20) μ m diam, yellowish- to blackish-brown, with smooth, c. 1–2 μ m thick wall. Anamorph absent.

Entyloma dactylidis is a world-wide, rather variable species parasitising a great number of species in the Gramineae belonging to the genera Agrostis, Aira, Alopecurus, Catabrosa, Cynosurus, Dactylis, Deschampsia, Festuca, Glyceria, Holcus, Hordeum, Koeleria, Phleum, Poa, Polygonum, Puccinellia, Trisetum. This complex species is characterized by its dark-coloured, densely packed, irregular spores, and it is clearly delimited towards other European Entyloma species.

In Hungary it was recovered on Deschampsia caespitosa (L.) Beauv., comit. Fejér, near Csákvár, "Dó-kút", alt. c. 150 m, 20. VI. 1961, S. TÓTH (BP, HUV 11355).

Tolyposporium junci (Schröter) Woronin, 1881 (1882): 577

Syn. Sorosporium junci Schröter, 1869. 6. Type on Juncus bufonius L., Germany, Silesia, Carlowitz near Breslau (Poland, Karlowice near Wrocław), IX. 1867, J. SCHRÖTER, in Schneider, Herb. schles. Pilze 94.

Sori (Fig. 5) external, tumour-like, forming a naked, black agglutinated to granular spore mass, composed of spore balls localized in the



Fig. 5. Sori of *Tolyposporium junci* (Schroter) Woronin in flowers and stems of *Juncus bufonius* L.

flowers (often involving only part of the inflorescence, the capsule, or only the base of the inflorescence and spreading to the adjacent bracts and rachis), less often in the base of the stems and basal leaves. Spore balls (Fig. 6) persistent, variable in form and size, globose, subglobose, elongate or irregular, 16–50(–80) μm long, opaque, dark reddish-brown to blackish-brown, composed of 3–40 or more spores. Spores (Fig. 7) subglobose to more or less angular, often rounded cuneiform and irregular, 6–13 x 8–17 (–20) μm , dark yellowish-brown to blackish-brown, smooth on the contact surface and provided with irregular warts on the free, slightly convex surface. The wall is unequally thickened (0.5–4 μm) and two-layered; in TEM

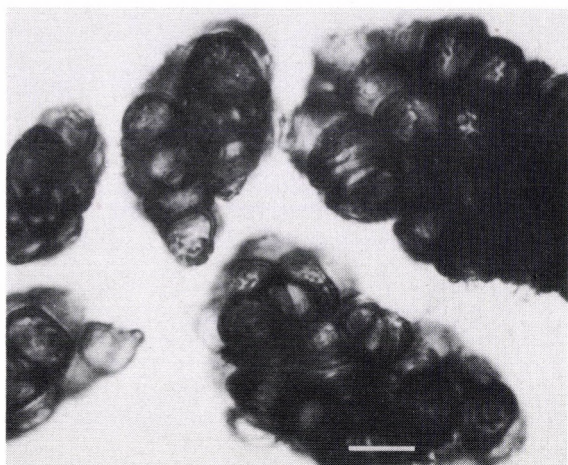


Fig. 6. Spore balls of Tolyposporium junci (Ványk, Ust. 107). Bar = 10 μ m

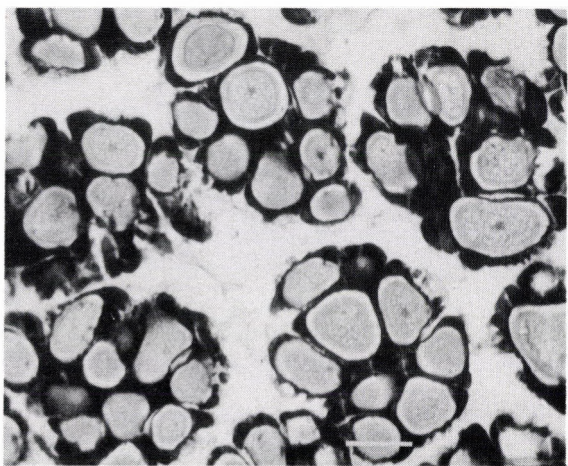


Fig. 7. Sections of spore balls and spores of Tolyposporium junci (Ványk, Ust. 107). Bar = 10 μ m

the inner layer appears to consist of a gray, equally thickened (0.6–0.8 μ m) internal layer and a light, unequal (0.2–1.2 μ m), peripheral layer, sharply delimited from the outer layer which appears black, unequal (0.2–2.5 μ m) and without distinct internal structure. The spores germinate in water after a resting period, usually producing four-celled promycelia with sporidia borne at the septa (WORONIN 1881 (1882): 575; BREFELD 1895: 150).

On Juncaceae: Juncus spp. Known from Europe and North America. In Hungary it was found on Juncus bufonius L., comit. Pest, Börzsöny Mountains, "Királyrét", 8. VII. 1986, J. GÖNCZÖL, E., T.U. and K. VÁNKY (BP, HUV 12214).

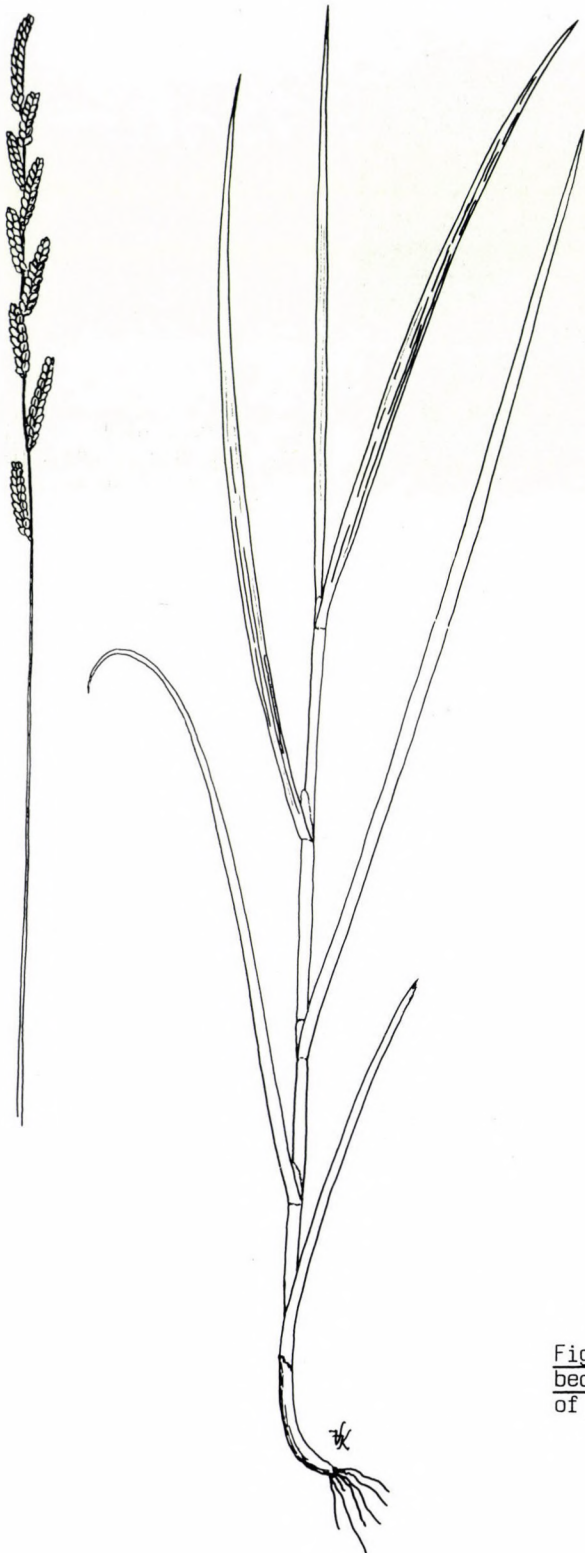


Fig. 8. Sori of Urocystis
beckmanniae Brezhnev in leaves
of Beckmannia eruciformis (L.)
Host.

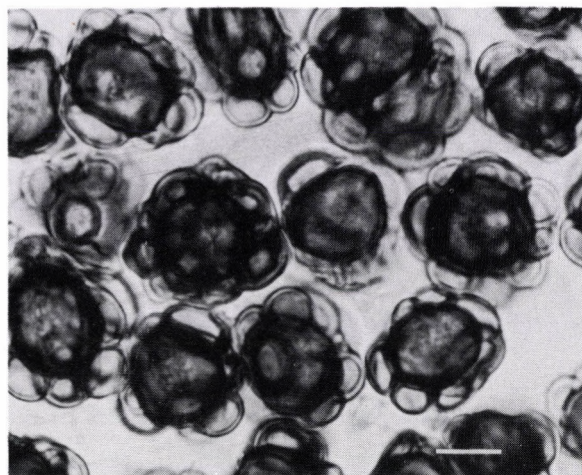


Fig. 9. Spore balls of Urocystis beckmanniae (Vánky, Ust. 477). Bar = 10 μ m

Urocystis beckmanniae Brezhnev, 1964: 196

Type on Beckmannia eruciformis (L.) Host, USSR, reg. Belgorod, Vorskla valley, "Les na Vorskle", 22. VI. 1953, I.E. BREZHNEV.

Sori (Fig. 8) in leaves and culms as striae between the veins, at first covered by the epidermis, which ruptures longitudinally revealing the powdery mass of spore balls. Spore balls (Fig. 9) composed of 1-2(-3) central spores surrounded by sterile cells. Spores globose to elongate, irregular and slightly angular, dark yellowish-brown, 12-13.5 \times 13.5-15 μ m. Sterile cells light yellow to olive-brown, globose to irregularly elongate, 3.5-6 \times 6.5-9 μ m.

On Gramineae: Beckmannia eruciformis (L.) Host. Known hitherto only from the type locality. In Hungary it was found in comit. Hajdú-Bihar, near Balmazújváros, "Kishortobágy", alt. c. 95 m, 24. VI. 1984, T., U. and K. VÁNKY (BP, HUV 11318). Distributed in VÁNKY, Ustilaginales exs. No. 477.

Urocystis luzulae (Schröter) Winter, in Rabenhorst, 1881: 120

Syn. Polycystis luzulae Schröter, in Cohn, 1877: 380. — Urocystis luzulae (Schröter) Schröter, in Cohn, 1887: 279. — Tubercinia luzulae (Schröter) Liro, 1922: 36. Type on Luzula pilosa (L.) Willd., Germany, Silesia, Jauer, "Buschhäuser auf den Hessbergen", coll. GERHARDT.

Sori (Fig. 10) in leaves usually restricted to the proximal parts of leaves, forming greyish-black striae between the veins, several cm in



Fig. 10. Sori of *Urocystis luzulae* (Schröter) Winter in leaves of *Luzula luzuloides* (Lam.) Dandy & Wilmott

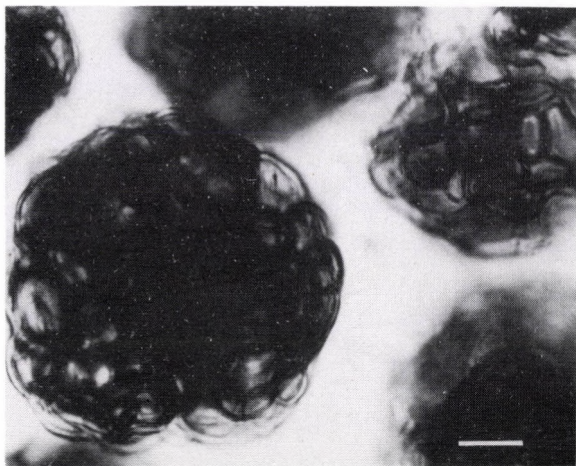


Fig. 11. Spore balls of *Urocystis luzulae* (Vánky, Ust. 479). Bar = 10 μ m

length, often confluent, at first covered by the epidermis which ruptures revealing the blackish-brown, powdery mass of spore balls. Spore balls (Fig. 11) globose to ovoid, 18–44 x 20–56 μ m, composed of 1–7(–12) spores surrounded by a continuous layer of sterile cells. Spores globose, subglobose to ovoid, 8–13.5 x (11–)12–16 μ m, chestnut-brown; wall c. 1.5 μ m thick, smooth. Sterile cells variable in size and form, 4–13 μ m long, with dark brown, thick wall (c. 1.5 μ m laterally and 0.5–0.8 μ m on the free surface), collapsing when dried.

On Juncaceae: *Luzula* spp. Known from a few places in Europe. In Hungary it was collected on *Luzula luzuloides* (Lam.) Dandy and Wilmott (= *L. albidula* (Hoffm.) D.C., which is apparently a new host for this smut), comit. Borsod-Abaúj-Zemplén, 20 km NE. Eger, Bükk Mountains, "Odorvár-hegy" near Bükkzsérc, alt. c. 500 m, 29. V. 1984, A. RÉVAY and J. GÖNCZÖL (BP, HUV 11319). Distributed in VÁNKY, Ustilaginales exs. No. 479.

Ustacystis waldsteiniae (Peck) Zundel, 1945b: 796

Syn. *Urocystis waldsteiniae* Peck, 1893: 112. — *Ustilago waldsteiniae* (Peck) Pazschke, in Rbh., Fgi. eur. 4011, 1895. — *Tuburcinia waldsteiniae* (Peck) Liro, 1922: 90. — *Whetzelia waldsteiniae* (Peck) Zundel, 1945a: 372. Type on *Waldsteinia fragarioides* (Michx.) Tratt., USA, New York, Albany Co, Alcove, VI. 1892, C.L. SHEAR, in Ellis and Ev., N. Amer. fgi. 2983; Shear, N.Y. fig. 86. — *Urocystis qei* Ellis and Everhart, 1900: 572. Type on *Geum ciliatum* Pursch., USA, Washington, Waitesburg, 7. V. 1900, R.M. HORNER (1430).



Fig. 12. Sori of Ustacystis waldsteiniae (Peck) Zundel in the veins of the leaves of Waldsteinia geoides Willd.

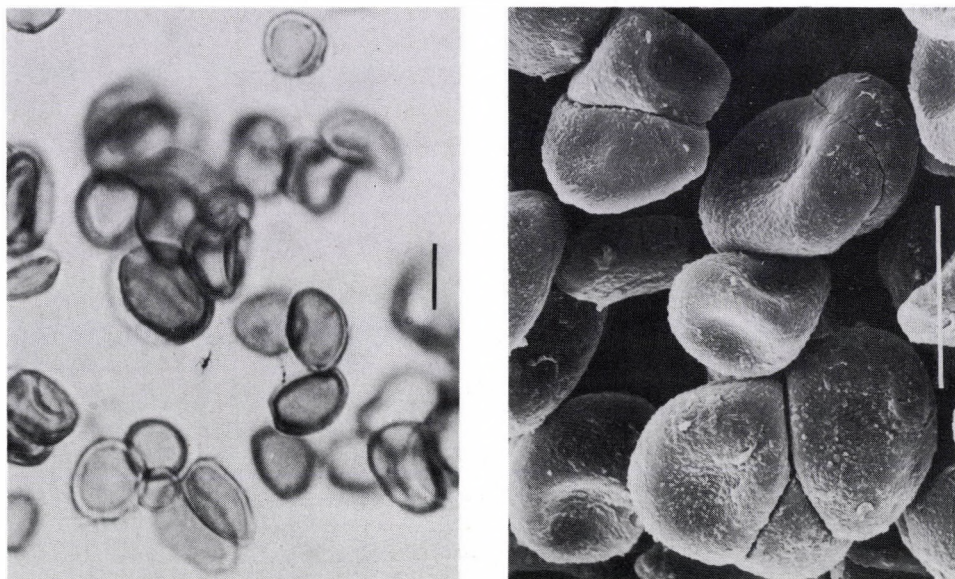


Fig. 13. Loose spore balls and spores of *Ustacystis waldsteiniae* in LM and in SEM (Vánky, Ust. 629).

Bars = 10 μ m

Sori (Fig. 12) in leaves, usually epiphyllous, following the veins, oval, linear or bifurcate, swollen, at first covered by a greyish peridium formed of host tissue and fungal elements, which at maturity splits longitudinally exposing the rather agglutinated, blackish-brown spore mass. Spores (Fig. 13) globose, subglobose, hemispheric, oblong or polyhedral to rather irregular, 7-12(-15) \times 9-15(-18) μ m in diam, single, in pairs or adhering together in groups of 3 or more, forming loose spore balls, reddish-brown, with sparsely situated, low rounded, hyaline warts. Sterile cells few or lacking, light yellowish-brown, attached to the spore balls. Germination by a septate, dicaryotic promycelium producing dicaryotic sporidia and mycelium (HANSON and ATKINSON 1938: 8).

On Rosaceae: Geum and Waldsteinia spp., known hitherto from North America and from a single find in Europe, in Transylvania (Roumania). In Hungary it was collected on Waldsteinia geoides Willd., comit. Borsod-Abaúj-Zemplén, between Aggtelek and Szinpetri, Bojamér valley, alt. c. 200 m, 21. V. 1987, J. GÖNCZÖL, U. and K. VÁNKY (BP, HUV 13196). Distributed in VÁNKY, *Ustilaginales* exs. No. 629.

ACKNOWLEDGEMENT

The authors gratefully acknowledge Dr. M. BERBEE (Davis, California, USA) for checking the English, and Mrs. C. SPECHT (Tübingen, Germany) for skillfully copying the photos.

LITERATURE

- Brefeld, O. (1895). Untersuchungen aus dem Gesamtgebiete der Mykologie. XII. Hemibasidii. Brandpilze III. — Münster i.W., Comissions-Verlag v.H. Schöningh, IV + 99-236 pp. + Pl. VI-XII.
- Brezhnev, I.E. (1964): (A new fungal species of the order Ustilaginales.) — Nov. Sist. Nizh. Rast, 1964: 196-197.
- Ciferri, R. (1924): Prima contribuzione allo degli Ustilaginales. — Bull. Soc. Bot. Ital. 1924: 46-59.
- Ciferri, R. (1928): Quarta contribuzione allo studio degli Ustilagniales. Ann. Mycol. 26: 1-68.
- Ellis, J.B., Everhart, B.M. (1900): New species of fungi from various localities. — Bull. Torrey Bot. Club 27: 571-578.
- Farlow, W.G. (1883): Notes on some Ustilagineae of the United States. — Bot. Gaz. 8: 271-278.
- Fischer von Waldheim, A. (19877): Aperçu systématique des ustilaginées, leurs plantes nourricieres et la localisation de leurs spores. Paris, 51 pp.
- Gutner, L.S. (1941): Golovnevye griby. (The smut fungi.) — Lenin Acad. Agric. Sci. Inst. Plant Protection. Moskow and Leningrad. 383 pp.
- Hanson, E.W., Atkinson, R.E. (1938): Preliminary studies on the cytology of *Urocystis waldsteiniae*. — Phytopathology 28: 8.
- Hariot, P. (1896): Note sur deux nouveaux champignons de France. — J. Bot. (Morot) 10: 299-301.
- Hariot, P., Patouillard, N. (1904): Description de Champignons nouveau de l'Herbier du Muséum. — Bull. Soc. Mycol. France 20: 61-65.
- Imre, K. (1985): Az *Entyloma linariae* Schroet. (Ustilaginales) előfordulása Magyarországon (The occurrence of *Entyloma linariae* Schroet. (Ustilaginales) in Hungary). — Bot. Közlem. 72: 145-149.

- Johanson, C.J. (19885): Svampar fran Island. — Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 41(9): 157–174.
- Lavrov, N.N. (1934): (Ustilagineae novae vel rariae Asiae septentrionalis.) — Trudy Tomsk. Gosud. Univ. 86: 83–87.
- Lavrov, N.N. (1937): (Tilletiaceae novae vel rariae Unionis Sovieticae). — Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kujbyseva 11: 1–4.
- Lavrov, N.N. (1938): (Tilletiaceae rariae eurasiaticae). — Trudy Biol. Inst. tomsk. Gosud. Univ. Kuybiseva 5: 43–85.
- Liro, J.I. (1922). Über die Gattung Tubercinika Fries. — Ann. Univ. Fenn. Abo. A.1(1): 1–153.
- Liro, J.I. (1938): Die Ustilagineen Finnlands II. — Ann. Acad. Sci. Fenn. Ser. A. 42(1): 1–720.
- Liro, J.I. (1939): Mycotheca fennica. Die Etiketten. No. 301–600. Helsinki, 136 pp.
- Moesz, G. (1950): A Kárpát-medence üszöggombái. (Les Ustilaginales du Bassin des Carpathes). — Budapest, Egyetemi Könyvkiadó, 255 pp.
- Peck, C.H. (1893): Urocystis waldsteiniae n. sp. — Annual Rep. New York State Mus. 46: 112.
- Rabenhorst, L. (1881): Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. 2. Aufl., 1. Pilze, I. Abt. Ustilagineae. pp. 79–131.
- Roumeguere, C., Saccardo, P. (1881): Reliquiae mycologicae Libertianae. — Rev. Mycol. (Paris) 3: 39–59.
- Saccardo, P.A. (1879): Fungi veneti novi v critici etc. Ser. X. — Michelia 1: 539–546.
- Savile, D.B.O. (1947): A study of the species of Entyloma on North American Composites. — Canad. J. Res., Sect. C, Bot. Sci. 25: 105–120.
- Schröter, J. (1869): Die Brand- und Rostpilze Schlesiens. — Abh. Schles. Ges. Vaterl. Cutl., Abth. Naturwiss. 1869/72: 1–31.
- Schröter, J. (1877): Bemerkungen und Beobachtungen über einige Ustilagineen. — In: Cohn, F., Beiträge zur Biologie der Pflanzen 2: 349–385.
- Schröter, J. (1887): Ustilaginei. — In: Cohn, F., Kryptogamen-Flora Schlesiens 3(1). p. 261–291.
- Vánky, K. (1985): Carpathian Ustilaginales. — Symbolae Botan. Upsal. 24(2): 1–309.
- Vánky, K., Gönczöl, J., Tóth, S. (1982): Review of the Ustilaginales of Hungary, with special regard to the results obtained after 1950. — Acta Bot. Acad. Sci. Hungar. 28: 255–277.
- Vánky, K., Tóth, S., Gönczöl, J., Révay, A., Imre, K. (1985): Seven species of Ustilaginales, new recorded from Hungary. — Acta Bot. Hungarica 31: 99–112.
- Viennot-Bourgin, G. (1927): Deux Entyloma dl'Ile de Madere. — Rev. Mycol. (Paris), N.S., 2: 118–124.
- Woronin, M. (1881/1882): Beitrag zur Kenntniss der Ustilagineen. — Abh. Senckenberg. Naturf. Ges. 12: 559–587.

Zundel, G.L. (1945a): Notes on a proposed new genus and four new species of the Ustilaginales. — Mycologia 37: 370–373.

Zundel, G.L. (1945b): A change in generic name. — Mycologia 37: 795–796.

REVISION OF THE GENUS JOVIBARBA AND CONSIDERATION OF THE SEDUM TECTORUM/
S. MARMOREUM COMPLEX AND S. MONTANUM SUBSP. CARPATICUM

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Specimens belonging to the genera Sempervivum and Jovibarba in Budapest (BP) have been examined. Lectotypes were selected for S. zeleborii Schott, S. pittonii Schott, Nyman and Kotschy, S. x barbulatum Schott, S. x funckii F. Braun and Koch, S. braunii Funck ex Koch in Sturm, S. assimile Schott, S. blandum Schott, S. laggeri Schott ex Hallier in Koch, S. debile Schott, S. schnittspahnii Lager and S. huterii Haussmann ex Seboth and F. Graf in Bennett. The taxonomic status of these taxa and of S. borisii Degen and Urumov, S. jakucsii Penzes, the S. tectorum L./S. marmoreum Grieseb. complex, S. montanum L. subsp. carpaticum Wettstein ex Hayek in Hegi and the species in the genus Jovibarba are also discussed. Two new combinations are made: Jovibarba hirta (Juslen. in L.) Opiz subsp. arenaria (Koch) J. Parnell comb. nov., Jovibarba hirta (Juslen. in L.) Opiz subsp. borealis (H. Huber) J. Parnell comb. nov.

INTRODUCTION

The genera Sempervivum L. and Jovibarba Opiz (Crassulaceae) are much in need of a comprehensive revision. The last monograph by PRAEGER was published in 1932 and since then a number of new species have been described some without reference to either living material or existing type specimens.

H.W. SCHOTT described a large number of new species of Sempervivum and Jovibarba. Schott's descriptions, though comprehensive, were published in books or journals not now readily available. This, combined with the fact that his herbarium was thought to have been destroyed during the Second World War (RIEDL 1965) has hampered typification and revision in these genera. Fortunately only the part of SCHOTT's herbarium housed at Vienna (W) was lost and in 1975 it was discovered that Budapest, (BP), contains a large part (perhaps all) of his personal herbarium (See SZUJKÓ-LACZA (1975) and PARNELL and SZUJKÓ-LACZA (1987)). This collection is ideal material for the lectotypification of SCHOTT taxa.

Many of SCHOTT's species were reduced to synonymy by PRAEGER (1932). However some of SCHOTT's species are pivotal to species complexes which have only recently been recognized and therefore lectotypification of all his species becomes very important.

BP is very rich in material from such centres of diversity of Sempervivum and Jovibarba as the Alps, Carpathian and Tatra mountain ranges. So in addition to the Schott material of these genera in BP there is also a limited amount of type material from other collectors.

In the first part of this paper I detail all Sempervivum and Jovibarba types in BP. For each species I nominate, where appropriate, a lectotype, transliterate any information present on the type sheet, discuss its current taxonomic status and where I do not reduce it to synonymy but maintain it at a rank above varietal rank give a photograph. Generally this section follows the layout of BURDET et al. (1981, 1982, 1983a and 1983b) who detailed BOISSIER and REUTER's nomenclatural types from Iberia in G.

There are some caveats on the information I provide. Firstly as nearly all of the SCHOTT specimens are stamped "Ex Herbario SCHOTT" and "Herbarium Archiepiscopi Dr. LUDOVICI HAYNALD" I do not specify this for each individual discussed. Additionally though I quote accession numbers, which are present on most sheets in BP, some sheets have no number or only a partly legible one which obviously cannot be quoted. Equally unfortunately I am in some cases quite unable to transliterate parts of some of the labels and where the transliteration remains doubtful I have indicated this with question marks.

Many labels bear both localities and "cult" on them; all in SCHOTT's handwriting (BURDET et al. (1978), PARNELL and SZUJKÓ-LACZA (1987)). I interpret this combination to mean that the specimens were cultivated by SCHOTT from rosette or seed material sent to him from the localities indicated. Because Semperviva are monocarpic it is most likely that they are the specimens he had in front of him when he drew up a particular description. In many cases it is obvious from the description that he worked from living material.

In the second section I discuss the status of the genus Jovibarba and also that of S. marmoreum Griseb. and S. montanum L. subsp. carpaticum Wettstein ex Hayek in Hegi.

In the third and final section I list the taxa I recognise in Jovibarba (to sub-specific level) and formally list the nomenclatural changes necessitated by this study.

SECTION 1

TYPIFICATION

1. SEMPERVIVUM ZELEBORII Schott in Österreichisches Botanisches Wochenblatt, Wien 7: 245-246 (1857).

TYPUS: "in Serbia /Zelebor/"

LECTOTYPUS

a) Annotation: "Serbian, Mt. Stoll, Cult".

b) Accession no. 148977.

Obs.: a. The lectotype is the top left-hand specimen, all other specimens on this sheet are isotypes. Fig. 1.

b. The specific epithet zelebori as published by SCHOTT must be treated as an orthographic error for zeleborii according to VOSS et al. (1983).

c. The lectotype differs from the currently accepted interpretation of S. zeleborii (MUIRHEAD (1966)) in its smaller flowers (max. 1.5 cms c.f. 2.5 cms), its broadly triangular rather than ovate to ovate-lanceolate calyx segments, its discreet, slightly concave nectarial scales (0.5 x 0.1 mm) and carpels which are glandular-hairy only upto the base of the style and not beyond. Additionally the leaves have hairs of two distinct lengths (0.5 & 1 mm) rather than the uniform pubescence suggested by the illustrations in MUIRHEAD (1966).

d. Lectotypification confirms the hypothesis of MUIRHEAD (1966) that S. zeleborii is a distinct taxon from S. ruthenicum Schnittsp. & Lehm.

2. SEMPERVIVUM PITTONII Schott, Nyman and Kotschy in Analecta botanica Vindobonae 19: (1854).

TYPUS: "In Styria"

LECTOTYPUS:

a) Annotation: "Styria, Cult".

Obs.: a. The lectotype is the top left-hand specimen, all other specimens on the sheet are isotypes except that in the bottom right-hand corner which is a specimen of S. montanum. Fig. 2.

b. There has been considerable confusion in the literature as to exactly what SCHOTT meant by S. pittonii. NEILREICH (1868), who analysed the species described by SCHOTT (1854), states that PITTONI found this species at Kraubat growing on serpentine; however SCHOTT (1854) makes no

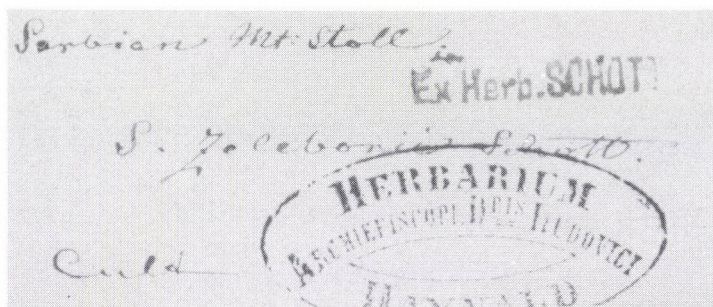


Fig. 1.

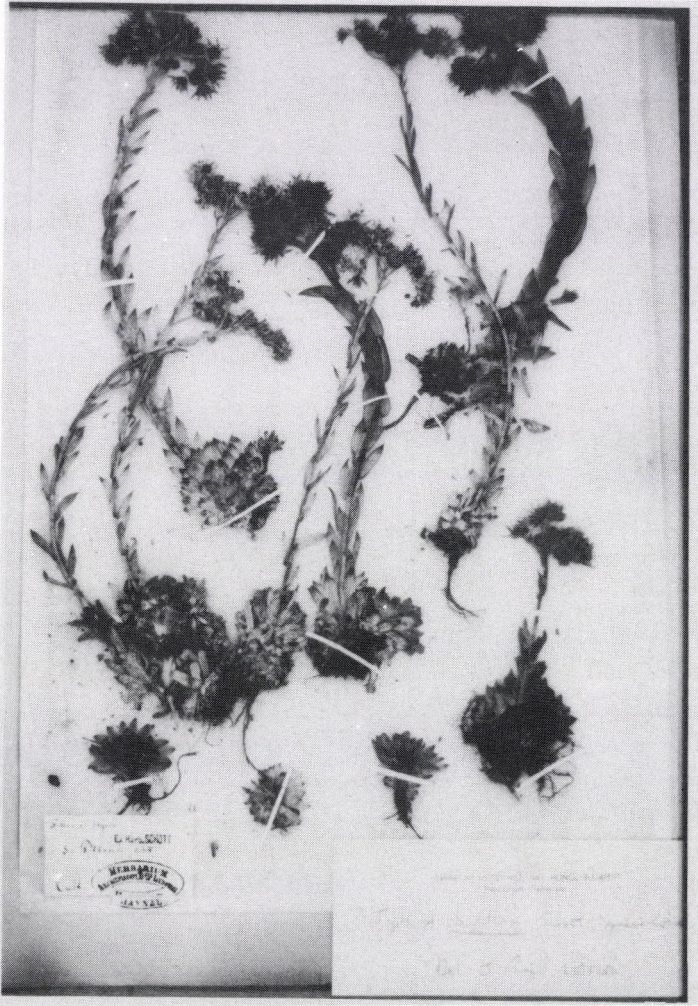


Fig. 2.

mention of Kraubat or serpentine. NEILREICH also states that PITTONI originally distributed this plant under the name Sempervivum braunii Funck ex Koch in Sturm (S. braunii is an albino variant of S. montanum) and that he (Neilreich) feels S. pittonii to be synonymous with S. braunii. This view is opposite to that of PRAEGER (1932) and most current workers who accept them as separate taxa. However, only NEILREICH examined the type specimen. Fortunately he appears to have been wrong as my re-examination of the lectotypes proves S. pittonii to be a separate species from S. braunii and hence S. montanum.

3. SEMPERVIVUM X BARBULATUM Schott in Österreichisches Botanisches Wochenblatt Gemeinnütziges Organ ... 3: 91 (1853).

TYPUS: "Monte Rosse der karnische-venetianischen Alpen"

LECTOTYPUS:

a) Annotation: "Cult. Kv".

b) Accession number: 148692.

Obs.: a: The lectotype is the second specimen from the bottom left-hand corner of the sheet. The other specimens are not isotypes. Fig. 3.

b. S. x barbulatum is the hybrid between S. arachnoideum L. and S. montanum.



Fig. 3.

4. SEMPERVIVUM X FUNCKII F. Braun and Koch in Flora 15: 4 tab. 1. (1932).

TYPUS: "Malnitzer Tauern"

LECTOTYPUS:

a) Annotation: "Malnitzer Tauern in Karnten, Bayreuth, Fr. BRAUN".

b) Accession number: 14787.

Obs.: a. The lectotype is the bottom left-hand specimen. The specimen immediately to the right of the lectotype is an isotype. The other specimens on the sheet cannot be considered as isotypes because of the additional and illegible label below them; though this label may be an earlier version of the lectotype label. Fig. 4.

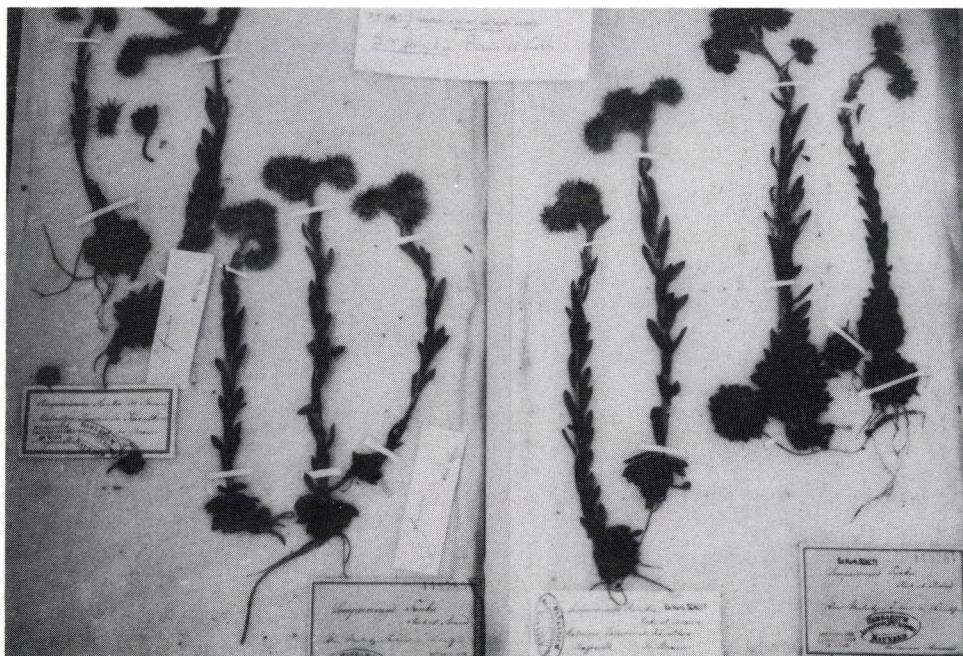


Fig. 4.

b. S. x funckii is the triple hybrid S. arachnoideum x S. montanum x S. tectorum.

5. SEMPERVIVUM BRAUNII Funck ex Koch in Sturm in Deutschlands Flora ed 1 6: Section 11 (1835).

TYPUS: "Grosglochner"

LECTOTYPUS:

a) Annotation: "Bayreuth, ?Birterzen? Alpe am Glochiner in Kairhein. Fr. Braun, 1834, S. braunii Koch and Funck. Cult."

Obs.: a. The lectotype is the bottom left-hand specimen. The specimen immediately to its right is an isotype as are the two immediately above and all three on sheet 148753.

b. S. braunii is best considered a form of S. montanum L. being a white flowered variant of it (i.e. forma braunii (Funck) Praeger).

6. SEMPERVIVUM ASSIMILE Schott in Österreichisches Botanisches Wochenblatt Gemeinnütziges Organ ... 3: 19-20 (1853)

TYPUS: "Vorkommen in Siebenburgen (Kotschy)"

LECTOTYPUS:

a) Annotation: "Propre Hermannstadt, 1850. Legit Th. KOTSCHY".

b) Accession number: 77392.

Obs.: a. The lectotype is the left-hand specimen on the sheet. The other specimen is not a type.

b. S. assimile forms part of the S. marmoreum Greisbach complex. The lectotype is glabrous with strong marginal cilia (See Section 2) and may warrant recognition at the forma level in the same way as S. blandum Schott (See below).

7. SEMPERVIVUM BLANDUM Schott in Österreichisches Botanisches Wochenblatt Gemeinnütziges Organ ... 3: 29-30 (1853)

TYPUS: "Vorkommen Siebenburgen (KOTSCHY)"

LECTOTYPUS:

a) Annotation: "In australii alpium tracta alt. Riasuby???" 17th Aug 1850. Legit Th. KOTSCHY."

b) Accession number: 77380.

Obs.: a. The lectotype is the bottom left-hand specimen on the sheet. The other specimens are not isotypes.

b. S. blandum forms part of the S. marmoreum complex. The lectotype has short hairs (See Section 2) and may warrant recognition at the forma level in the same way as S. assimile (See above).

8. SEMPERVIVUM LAGGERII Schott ex Hallier in Koch in Synopsis der deutschen und schweizer Flora ed. 3 1: 944 (1892) Leipzig

TYPUS: "Switzerland"

LECTOTYPUS:

a) Annotation: "Helvet., LAGGER. S. Laggeri Schott".

Obs.: a. The lectotype is the second specimen from the left in the top row.

b. All other specimens on this sheet cannot be considered as isotypes as they seem to be backcrosses of the hybrid S. arachnoideum x S. tectorum with S. arachnoideum.

c. S. laggerii is a synonym of S. arachnoideum L.

9. SEMPERVIVUM DEBILE Schott in Österreichisches Botanisches Wochenblatt Gemeinnütziges Organ 2: 18 (1852).

TYPUS: "Westlichen Tirol"

NEOTYPUS:

a) Annotation: "Br. Sem debile Schott".

b) Accession number: 14875.

Obs.: a. The neotype is the left-hand specimen and the other specimen is an isotype.

b. S. debile is a synonym of S. montanum.

10. SEMPERVIVUM SCHNITTSPAHNII LAGGER IN Flora 41: 659 (1858)

TYPUS: "Wachst im Visperthal, Ober-Wallis, zwischen Stalden und Rauda"

LECTOTYPUS:

a) Annotation: "Zermatt Dr. Lagger"

b) Accession number: 148998.

Obs.: a. The lectotype is the only specimen of the sheet.

b. S. schnittspahnii is a synonym of S. c fauconetii Reuter (see 12 below).

11. SEMPERVIVUM HUTERII Haussmann ex Seboth and Graf in Bennett in Alpine Plants ed. Bennett 4: 45 and Plate 90 (1876)

TYPUS: "Rocky, stony places on the argillaceous alps. Central chain of the Alps especially the high ridges in Tyrol and Carthina"

LECTOTYPUS:

a) Annotation. "Tirol; Alpes graniti in Isica"

b) Accession number: 148826.

Obs.: a. The lectotype is the second specimen from the top right-hand corner. The specimen to its right is an isotype, those to its left are not.

b. S. huterii is a synonym of S. x rupicolum Kerner in Ferdinand, the hybrid between S. montanum and S. wulfenii Hoppe.

12. SEMPERVIVUM PILIFERUM Jordan in Observations sur plusieurs plantes nouvelles, rares ou critique de la France 7: 27-29 (1849)

TYPUS: "Rabou pres du Gap"

ISOTYPUS:

- a) Annotation: "Hautes Alpes, Rabou, pres Gap July 1835 leg. A. JORDAN

Obs.: a. JORDAN's main collections are in Lyon and the lectotype should be selected from that material.

b. S. piliferum is a synonym of S. x fauconetii Reuter the hybrid between S. arachnoideum and S. tectorum L.

13. SEMPERVIVUM BORISII Degen and Urumov in Magyar Botanikai lapok 13: 176-177 (1915)

HOLOTYPUS:

- a) Annotation: "Ad Pancercevo non procul Sofia Leg. I. K. URUMOV. 1914."

b) Accession number: 469830.

Obs.: a. S. borisii is a synonym of S. ciliosum Craib published 3 days earlier.

14. SEMPERVIVUM JAKUCSII Péntzes in Annales Historico-Naturales Musei Nationales Hungarici (Bot.) 57: 169-171 (1965)

HOLOTYPUS:

- a) Annotation: "In rupestribus calcareis mt. Mali That intera pag. Pojanet Podgerje, ad app. Korca. 16/VII/1960. Leg. P. JAKUCS."

Obs.: a. S. jakucsii is a synonym of S. ciliosum. It is a short stolonated version of the "Mali That form" of that species (S. ciliosum Craib var. galicium A.C. Smith).

In addition to the above validly and effectively published material there are three taxa whose names commonly appear in herbaria but which seem be never to have been validly or effectively published.

15. SEMPERVIVUM HISPIDULUM Schott in Schedula No. 486. nom nud.

Obs.: S. hispidulum specimens are usually S. montanum.

16. SEMPERVIVUM GLACIALE Braun in Schedula. nom nud.

Obs.: S. braunii specimens are usually S. montanum.

17. JOVIBARBA BRASSII Schott & Kotschy in Schedula. Nom nud.

obs.: a. S. brassii specimens are usually Jovibarba heuffelii (Schott) A. & D. Love. See below.

Unfortunately I was unable to locate potential type material of the many other Sempervivum and Jovibarba species which were described by SCHOTT. There are 36 sheets in BO additional to those detailed above which come from SCHOTT's personal herbarium. However, they are unnamed and often bear no localities or dates. It is likely that they could be used as neotype or lectotype material for some of the other SCHOTT taxa but I am unwilling to do so as yet.

SECTION 2

DISCUSSION OF THE STATUS OF JOVIBARBA, S. MARMOREUM and S. MONTANUM SUBSP. CARPATICUM

The extensive collection in BP allows a clear assessment of the status of the variation in the S. marmoreum/S. tectorum complex, in S. montanum subsp. carpathicum and in the genus Jovibarba.

JOVIBARBA

Jovibarba Opiz (1852) was thought by HUBER (1966) (on the authority of H.P. FUCHS) to be an invalid generic name. HUBER therefore substituted the next most recently published valid name at generic rank (Diopogon Jourdan and Fourret) when he partly revised the genus making a number of Jovibarba species into sub-species. However WEBB (1961, 1964) (on the authority of DANDY) and HOLUB (1967) both argue that Jovibarba was validly published, with which opinion I concur.

Jovibarba is a very variable genus containing, according to WEBB (1964), five species: J. allionii (Jordan and Fourr.) D.A. Webb, J. arenaria (Koch) Opiz, J. hirta (L.) Opiz, J. sobolifera (J. Sims) Opiz and J. heuffelii (Schott) A. and D. Löve.

J. allionii and J. arenaria are distinguished from each other largely on the basis of their rosette colour and the distribution of glandular hairs on the rosette leaves.

According to WEBB (1964) there are two subspecies of J. hirta:

subsp. hirta and subsp. glabrescens (Sabr.) Soó and Jávorka. These taxa are distinguished from each other by their cauline leaves and sepals being hairy or glabrous and their disjunct distributions (westerly or easterly) respectively. Unfortunately not only are there many intermediates in BP but the distribution of the glabrous and hairy variants overlaps. A similar condition pertains in J. heuffelii (Zonneveld (1982)). The distinction between J. sobolifera and J. hirta is based on the openness of the rosette and whether the leaves are obovate-oblongate or broadly lanceolate. Examination of material in BP indicates that these characters are not strongly correlated. Additionally, the glaucous leaved J. hirta var. hillebrandtii from Gulsen (Yugoslavia) is described (ZONNEVELD (1981)) as having oblongate rosette leaves with nectar scales longer than broad — both characteristics of J. sobolifera. It is clear that these two species warrant reduction to sub-specific rank.

Indeed all five species of Jovibarba in WEBB (1964) are very closely related to each other; the most distinct species being J. heuffelii. HUBER (1966) makes the other four species (excluding J. heuffelii) into subspecies of Diopogon hirtus. SOÓ (1972) then re-made some of these combinations in Jovibarba hirta (Julsen) Opiz though he also places Sempervivum hirtella Schott (a nomen subnudum) and Sempervivum neilreichii Schott, Nyman and Kotschy in J. hirta as additional sub-species. I agree with HUBER (1966) but it is essential to re-make the combinations in the valid genus i.e. Jovibarba.

SEMPERVIVUM

S. marmoreum is a very variable species. Undoubtedly its closest relation is S. tectorum L. from which it differs in its usually pubescent leaf rosettes. Examination of material in BP showed that S. marmoreum exists in three forms. Firstly a glabrous form lacking pubescence on the rosette leaves but usually with distinct marginal cilia (first described by SCHOTT under the name S. assimile); secondly a pubescent form with short (c. 2 mm) hairs on the leaf surface and marginal cilia (first described by SCHOTT under the name S. blandum); thirdly a weakly or strongly pubescent form with long (c. 4 mm) hairs on the leaf surface. There is no other distinction that I can see between these different forms of S. marmoreum. Indeed some sheets (from the Pilis mountains) contain a mixture of long and short haired plants all collected from the same locality. These forms,

which differ solely in their degree of pubescence, may warrant recognition at the forma level but certainly not at varietal or subspecific rank. As the glabrous specimens in BP appear to be indistinguishable from S. tectorum L., S. marmoreum is probably best treated as a sub-species of S. tectorum.

S. montanum subsp. carpathicum is a large flowered variant of S. montanum. There are two forms of material from the Carpathians. Firstly a large flowered (c. 16 mm diameter or more) sparsely hairy form which corresponds to subsp. carpathicum; secondly a more strongly hairy smaller flowered form (c. 10 mm diameter or less) which is indistinguishable from ordinary S. montanum ($2n = 42$). The large flowered form is close to S. montanum subsp. stiriacum (Wettstein ex Hayek) Hegi et Schmidt in Hegi ($2n = 84$) and cannot be satisfactorily distinguished from it morphologically. Chromosomal counts must be obtained to enable the status of large flowered Carpathian material to be determined.

SECTION 3

REVISION OF JOVIBARBA

In this section I cite the basionym and the principal synonyms only.

JOVIBARBA

1. Jovibarba hirta (Juslen. in L.) Opiz Seznar 55 (1852)

Basionym

Sempervivum hirtum Juslen. in L. Cent. Pl. 1 12 (1755).

Webb (1964) cited this as J. hirta (L.) Opiz though ROTHMALER had in 1943 attributed the authorship of Centuria 1. plantarum (1755) to Juslenius (see STAFLEU and COWAN (1983).

Synonym

Diopogon hirtus (Juslen. in L.) H.P. Fuchs ex Huber
subspecies:

1. Jovibarba hirta (Juslen. in L.) Opiz subsp. hirta

Jovibarba hirta (Juslen. in L.) Opiz subsp. glabrescens (Sabr.) Soó and Jávorka in Favarger and Zesiger (1964) in Flora Europaea 1 (1964) comb. incerta.

2. Jovibarba hirta (Juslen. in L.) Opiz subsp. allionii (Jordan and Fourreau) Soó in Feddes Repert. 83: 174 (1972).

Basionym

Diopogon allionii Jordan and Fourreau in Brev. Plant. Nov. fasc. 2: 46 (1868)

Synonyms

Sempervivum allionii (Jordan and Fourreau) Nyman Consp. Fl. Eur. 260 (1879).

Diopogon hirtus (Juslen. in L.) H.P. Fuchs ex H. Huber subsp. allionii (Jordan and Fourreau) H. Huber in Hegi Illust. Fl. Mittel. ed.3. 3.2a 104-105 (1966).

3. Jovibarba hirta (Juslen. in L.) Opiz subsp. arenaria (Koch) J. Parnell comb. nov.

Basionym

Sempervivum arenarium Koch Syn. Fl. Germ. ed. 1 833 (1837).

Synonyms

Diopogon hirtus (Juslen. in L.) H.P. Fuchs ex Huber subsp. arenarius (Koch) H. Huber in Hegi Illust. Fl. Mittel. ed.3. 3.2a 105 (1966).

Sempervivum neilreichii Schott, Nyman and Kotschy Analecta Botanica 19 (1854). This is merely a form with glabrous stem leaves and narrow rosette leaves which is connected by numerous intermediates with the type.

4. Jovibarba hirta (Juslen. in L.) Opiz subsp. borealis (H. Huber) J. Parnell comb. nov.

Basionym

Diopogon hirtus (Juslen. in L.) H.P. Fuchs ex H. Huber subsp. borealis Huber in Hegi Illust. Fl. Mittel. ed.3. 3.2a 107-108 (1966).

Synonyms

Jovibarba sobolifera (J. Sims) Opiz Seznam 54 (1852).

Sempervivum soboliferum J. Sims Bot. Mag. 1457 (1812).

Jovibarba hirta (Juslen in L.) Opiz subsp. hirtella (Schott) Soó in Feddes Rept. 83: 174 (1972).

5. Jovibarba heuffelii (Schott) A. and D. Löve in Bot. Not. 114: 39 (1961).

Basionym

Sempervivum heuffelii Schott in Oster. Bot. Woch. 2: 18 (1952).

Synonyms

Jovibarba heuffelii (Schott) A. and D. Löve subsp. patens (Griesb. et Schenk) HOLUB in Folia Geobot. Phytotax. 8: 176-177.

SUMMARY

Examination of specimens belonging to the genera Sempervivum and Jovibarba in BP revealed a number of types. Lectotypes were selected for S. zeleborii Schott, S. pittonii Schott, Nyman and Kotschy, S. x barbula-tum Schott, S. x funckii F. Braun and Koch, S. x braunii Funck ex Koch in Sturm, S. assimile Schott, S. blandum Schott, S. laggeri Schott ex Hallier in Koch, S. debile Schott, S. schnittspahnii Lagger and S. huterii Haussmann ex Seboth and F. Graf in Bennett and their taxonomic status discussed. The first seven taxa are still maintained the rest being reduced to synonyms. Examination of the holotypes of S. borisii Degen and Urumov and S. jakucsii Péntzes show them to be synonyms of S. cilliosum Craib. S. tectorum L. and S. marmoreum Griseb. form a species complex and S. marmoreum is probably best treated as a sub-species of S. tectorum. S. montanum L. subsp. carpaticum Wettstein ex Hayek is suggested to be conspecific with S. montanum subsp. stiriaticum. Discussion of the variation pattern of species in Jovibarba indicates that four of the currently recognised five species are best treated as sub-species. The necessary two new combinations are made: Jovibarba hirta (L.) Opiz subsp. arenaria (Koch) J. Parnell comb. nov., Jovibarba hirta (L.) Opiz subsp. borealis (H. Huber) J. Parnell comb. nov.

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REFERENCES

- Burdet, H.M., Charpin, A., Jacquemoud, F. (1981): Types nomenclatureaux des taxa iberiques décrits par Boissier ou Reuter. I. Gymnosperms a Gramineae. Candollea 36: 543-584.
- Burdet, H.M., Charpin, A., Jacquemoud, F. (1982): Types nomenclatureaux des taxa iberiques décrits par Boissier ou Reuter. II. Iradacées a Potamogetonacées. Candollea 37: 381-395.

- Burdet, H.M., Charpin, A., Jacquemoud, F. (1983a): Types nomenclaturaux des taxa iberiques décrits par Boissier ou Reuter. III. Acéracees a Chénopodiacees. Candollea 38: 401-441.
- Burdet, H.M., Charpin, A., Jacquemoud, F. (1983b): Types nomenclaturaux des taxa iberiques décrits par Boissier ou Reuter. IV. Cistacées a Composées. Candollea 38: 751-802.
- Holub, J., Pouzar, Z. (1967): A Nomenclatural Analysis of the Generic Names of Phaenerogams Proposed by F.W. Opiz in his Seznam Rostlin Ceske. Folia Geobot. Phytotax. (Praha) 2: 397-428.
- Huber, H.H. (1966): Gustav Hegi Illustrierte Flora von Mitteleuropa. IV 2a. Paul Parey, Berlin.
- Muirhead, C.W. (1966): Sempervivum globiferum. Notes Roy. Bot. Gard. Edin. 26: 279-285.
- Neilreich, A. (1868): Über Schott's Analecta botanica. Sitz. -Ber. Akad. Wiss., Wien 58: 552-574.
- Opiz, F.M. (1852): Seznam Rostlin Květeny České. Prague.
- Parnell, J., Szujkó-Lacza, J. (1987): H.W. Schott's personal herbarium in BP. Taxon 36: (In press)
- Praeger, R.L. (1932): An Account of the Sempervivum group. Royal Horticultural Society, London.
- Riedl, H. (1965): Heinrich Wilhelm Schott (1794-1865). Taxon 14: 209-213.
- Schott, H.W. (1854): Analecta Botanica. C. Gerold, Vienna.
- Soó, R. (1972): Systematisch-nomenklatorische Bemerkungen zur Flora Mitteleuropas mit Beziehungen zur sudosteuropäischen Flora. Feddes Rep. 83: 129-212.
- Stafleu, F.A. and Cowan, R.S. (1983): Taxonomic Literature IV. W. Junk. The Hague. (Regnum Vegetabile 110.).
- Szujkó-Lacza, J. (1975): What happened with Schott's herbarium. Ann. Hist.-nat. Mus. Nat. Hung. 67: 57-59.
- Webb, D.A. (1961): Crassulaceae. in Flora Europaea Notulae Systematicae ad Floram Europaeam spectantes 2. ed. V.H. Heywood. Separatum ad Feddes Repert. 68: 197-198.
- Webb, D.A. (1964): Jovibarba. in Flora Europaea. Eds: Tutin et al. Cambridge University Press. Cambridge.
- Voss, E.G., Burdet, H.M., Chaloner, W.G., Demoulin, Greuter, W.V., Hiepko, P., McNeill, J.C., Miekle, R.D., Nicholson, D.H., Rollins, R.C. and Silva, P.C. (1983): International code of Botanical nomenclature. Regnum Vegetabile 111: I-XV and 1-472.
- Zonneveld, B.J.M. (1981): Sempervivums of Karinthia and Styria. Bull. Alp. Gard. Soc. 49: 83-85.
- Zonneveld, B.J.M. (1982): Sempervivums in Bulgaria. Bull. Alp. Gard. Soc. 50: 117-120.

THE WHITE CLOVER (TRIFOLIUM REPENS L.) GENE POOL I.
TAXONOMICAL REVIEW AND PROPOSALS

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In order to demonstrate interrelations between taxonomy and genetics in the case of a wild and cultivated species, the variability described by botanists for white clover has been reviewed in this first part of the paper. The genes of taxonomical importance identified in white clover gene pool will be listed in the second part.

In this part the taxon names used mostly by Central-European authors working in the genetic centre of the species have been compiled in an alphabetical synopsis. The differentiation process of the cultivated populations has been detected using the nomenclature adopted between 1651 (!) - 1985 in different countries for the designation of different variety groups.

Based on literature review, herbarium specimens and field experiments, consistent nomenclatural solutions have been proposed for the whole white clover gene pool, which seems to consist on primary level (GP-1) from 8 spontaneous subspecies and 4 major cultivar groups (convarietas), on the secondary level (GP-2) from 6 or 7 species.

The proposed taxa are considered as Operational Taxonomic Units (OTU), i.e. a nomenclatural category based on traditional and modern (genetical, numerical etc.) methods for the delineation and denomination of different compartments of a gene pool.

INTRODUCTION

Taxonomy, genetics and evolution science are strongly interrelated - the taxonomic problems of some "interspecific" crosses are well known for the specialists concerned. The gene pool concept (HARLAN et DE WET 1971 ap. SZABÓ 1983) is based mainly on the taxonomic categories, too. A case study on the white clover (Trifolium repens L.) taxonomy illustrates well these interrelations.

White clover is one of the most important forage legume species in temperate grasslands (CSÚRÖS et al. 1973, DUKE 1981, SPEDDING et al. 1972,

TAYLOR 1985 etc.) evolving strongly under the pressure of selection and breeding. In Central Europe wild white clover populations are widely distributed on different — even contrasting — habitats from the sea shores and plains up to the highest peaks of the Carpathians. This region has been considered as one of the genetic centres for white clover (TAYLOR l.c.). According to VAVILOV 1951, and ZEVEN et ZHUKOVSKI 1975 the centre of origin of white clover seems to be in the Mediterranean region. These Mediterranean populations have been selected, mostly, for cultivation in America, as well as in Australia. Another secondary centre is situated perhaps in The Netherlands.

Trifolium repens is an allogamous species with a complicated auto-incompatibility system. Outstanding vegetative and good generative reproduction are characteristic strategies. The majority of the examined populations has been found to be on tetraploid level ($2n = 4x = 32$) but diploid and hexaploid populations have also been recorded (TAYLOR 1985, 1986, THIEMANN 1980). The inter- and intrapopulational genecological differentiation of the locally adapted populations is advanced, genetic heterogeneity is accordingly high, phenotypical plasticity and "sysiphusian fitness" is striking (BURDON 1985). Due to the genetic variability and phenotypical plasticity — complicated in cultivated populations by breeding and agricultural practices — white clover systematics is fascinating, but confuse and somewhat neglected. This is surprising because the different white clover taxa are widely used (and often misused) in genetical and ecological research. Trifolium repens L. has become, in the last period, an important laboratory plant, a kind of "Drosophila of the plant ecology".

The main purpose of this work is the review of the nomenclature proposed mostly by skilled Central European botanists and plant breeders for the white clover variability. The presented names may be considered (at last in part) as the taxonomic reflexion of microevolutional realities.

The genetic treatment of this variability by means of identified genes or gene frequencies found by different authors, according to the principles outlined first by DADAY(1954, ap. 1958) and stressed recently by other authors (DAVIS et al 1967, SZABÓ 1980, TAYLOR et al. 1985 etc.) will be the subject of another paper.

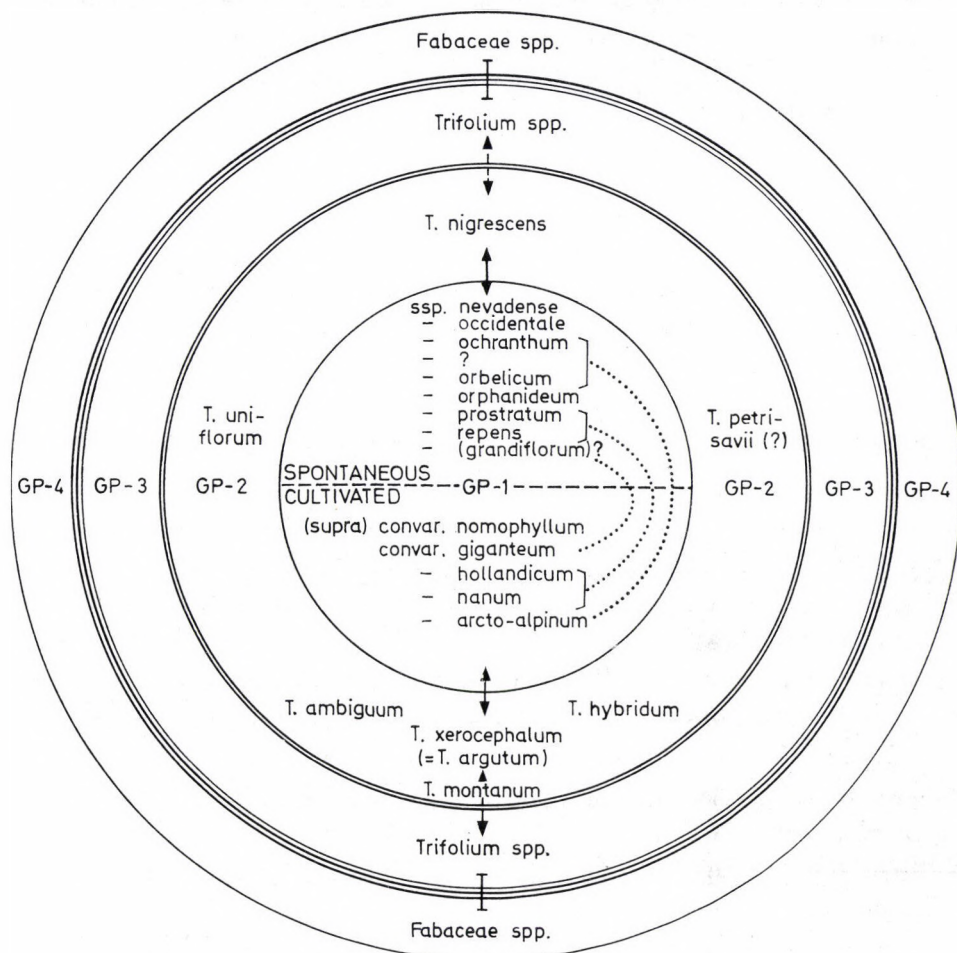


Fig. 1. The white clover (*Trifolium repens* L.) gene pool

MATERIAL AND METHOD

During the 1975–1985 period more than 500 wild and cultivated white clover accessions have been studied on the experimental fields of the Agronomy Institute Cluj-Napoca and in the Agrobotanical Garden of this institute, where the author formerly have been employed. Botanical and agronomical literature have been reviewed simultaneously in order to monitor the nomenclatural solutions used to describe the observed variability. These names have been arranged in an alphabetical order with the indication of the taxonomic level accepted in the source. The list was compiled in order to insure a quick orientation in names used by different authors and to reflect the white clover taxonomy outlined during the last two centuries.

Taxonomical solutions considered useful for the differentiation of the economically important white clover germplasm have been suggested according to the general principles of cultivar classification. The gene pool and germplasm concept has been used in accordance with HARLAN and DE WET (1971) and SZABÓ (1983).

RESULTS AND DISCUSSION

The variability of white clover reflected in taxonomical terms proposed for wild and cultivated populations has been presented in Table 1.

Table 1

Synopsis of the taxa described in the primary gene pool (GP-1) of the white clover — Trifolium repens L.

-
- alloideum Dore — DORE ap. TURKINGTON et al. 1983 pro forma (f.)
alpestre Guss. — GUSSONE 1827 pro var., ap. HEGI, SOÓ 1966
 idem, syn. var. biasolettii (Steud. et Hochst.) Aschers. et Graebn.,
T. biasolettianum Steud. et Hochst., T. neglectum Noe, T. monvernense
 Shuttlew.
alpinum Schur non L. — SCHUR 1866 pro specie (sp.), HEGI 1924 pro var., SOÓ
 1968 idem, syn. T. orphanideum Boiss. (species vicarians?), T. helveticum
 Scheele (sp. vic.), BELDIE 1977 pro subspecie (ssp.) syn. T. orphanideum
 auct. non Boiss.
alpinum (Schur) Rothm. — ROTHMALER?, BOŞCAIU 1971 pro ssp.
angustifolium Krösche — KRÖSCHE 1924 pro sp. ap. SOÓ 1966 pro lusum (l.)
angustiflorum SOÓ — SOÓ 1966 (?), BOROS et SZABÓ 1968 pro f. culta
arcto-alpinum h.l. — pro convarietas nova (convar. nova)
arenosum Dav. — DAVIDOV 1902 pro var., KOZUHAROV 1976 pro var. syn. f.
minus Bald. ex Rohl.
atropurpureum, erroneo atripurpureum hort. — HEGI 1924 pro "Glücksklee"
 (l.), BONSTEDT 1931 pro f., SOÓ 1966 idem, BOROS et SZABÓ 1968 idem.
biasolettii Steud. et Hoecht. — STEUDEL et HOCHSTENS 1927 (?), syn. biaso-
lettianum Steud. et Hochst. pro sp., HEGI 1924 pro var. syn. alpestre
 Guss., JULEN 1959 idem, COOMBE 1968 syn. pro var. prostratum Nyman.
bienne h.l. — pro provarietas nova (provar. nova)
caespitosum Domin — DOMIN 1932 ap. SOÓ 1966 pro f., BOROS et SZABÓ 1968,
 idem.
caespitosum Schur — SCHUR 1866 ap. A. NYÁRÁDY 1957 syn. pro var. orphanideum
 Boiss.
cultum Alef. — ALEFELD 1866 pro f. (var.?) ap. HEGI 1924 pro f. culta p.p.
 syn. f. macrocephalum Fiori et Paol., SOÓ 1966 syn. pro var. typicum A.
 et G. et pro f. giganteum hort., BARCHIKOWSKA 1976 ap. VACEK et al.
 1982 pro f.
foliatum Rigo — ex. Herb. Haussknecht
galerosum Grec. — GRECESCU ap. A. NYÁRÁDY 1957 syn. pro var. obcordatum
 E. Nyár.
galerosum Schur — SCHUR 1866 pro sp., non Schleich. !, ap. A. NYÁRÁDY syn.
 pro T. transsilvanicum Schur

Table 1 (cont.)

- genuinum Aschers. et Graebn. (A. et G.) — ap. HEGI 1924 syn. pro var.
typicum A. et G. = var. genuinum f. typicum et syn. pro f. sylvestre
 Alef. ap. A. NYÁRÁDY pro f. (1957)
- giganteum Lagr. — Foss. — LAGREZE-FOSSAT 1847 pro sp., HEGI 1924 pro f.,
 syn. var. typicum f. giganteum, SOÓ 1966 pro f. syn f. lodigense hort.,
 A. NYÁRÁDY idem HEGI 1924, BOROS et SZABÓ 1968 f. pro ssp. repens syn.
lodigense hort., CSÚRÖS et RESMERIJA 1973 idem, ZEVEN et ZHUKOVSKY 1975
 pro var. cum "Lodi clover", "Ladino clover", S.U.K. 1977 pro f., VACEK
 et al. idem (1982), CLEVELAND 1985 pro var., SZABÓ 1988. em. h.l. pro
 convar., convar. nova.
- gracillimum, erroneo gracillinum, Schur — SCHUR 1866 pro sp. ap. A. NYÁRÁDY
 1957 pro f., SOÓ 1966 idem syn. f. minus Bald. et Rohl.
- grandiflorum Peterm. — PETERMANN 1846 pro var. ap. A. NYÁRÁDY 1957 pro f.,
 sec. HEGI 1924, SOÓ 1966 idem syn. var. typicum A. et G. f. giganteum
 hort. (!), BOROS et SZABÓ 1968 f. pro ssp. repens.
- helveticum Scheele — SCHEELE 1843 pro sp., ap. HEGI 1924 syn. pro var.
alpinum Schur
- hollandicum Erith — ERITH 1921 ap. NYÁRÁDY A. 1957 pro f., SOÓ 1966 idem,
 BOROS et SZABÓ 1968 f. pro ssp. repens, S.U.K. 1977 pro f., VACEK et al.
 1979, 1982 idem, SZABÓ em. h.l. pro convar., convar. nova.
- ladino hort. — HEGI 1924 pro f. hort., BRACHIKOVSKA 1976 ap. VACEK et al.
 1982 pro f. syn. f. giganteum
- limonium Phil. — PHILIPPI 1856 pro sp. ap. MANSFELD 1959, 1986 syn. pro
T. repens L.
- lodi hort. — HEGI 1924 pro f. hort. syn. pro f. giganteum
- lodigense hort. — HEGI 1924 pro f., syn. pro f. giganteum, SOÓ 1966 idem.
- longipes Peterm. — PETERMANN 1846 ap. HEGI 1924 pro f., syn var. typicum,
 SOÓ 1966 idem et pro lusu, BOROS et SZABÓ 1968 idem
- luxurians DC. — J. BAUHIN 1651 (!!) in Historia plantarum universalis ap.
 A.P. DE CANDOLLE 1825
- macrocephalum Fiori et Paol. — FIORI et PAOLETTI pro sp. ap. HEGI 1924 pro
 var., syn. pro f. cultum, SOÓ 1966 idem, syn. pro f. giganteum hort.
- microphyllum Lagr.-Foss. — LAGRESE-FOSSAT 1847 pro var. ap. HEGI 1924 pro
 f. syn. pro var. prostratum DC. et Lam. non Biasol. nec Nyman, A.
 NYÁRÁDY 1957 idem, syn. pro var. minus Gib. et Belli, SOÓ 1966 idem,
 BOROS et SZABÓ 1968 pro f. syn. var. prostratum Schur
- minus Bald. ex Rohl. — BALDACCI ex ROHLENA 1911, ap. SOÓ 1966, 1970 pro f.,
 syn. pro f. gracillimum Schur
- monstruosum Fr. Zimm. non Gaudin, erroneo monstruosa — ZIMMERMANN ap. SOÓ
 1966 pro f.
- monstruosum Gaudin — GAUDIN 1929 ap. SOÓ 1966, 1968 pro f., syn. pro f.
phyllanthum Ser.; et auct. dif. in herb. dif. monvernense Shutlew.
- nanum h.l. — pro convar., convar. nova
- neglectum Noe — NOE pro sp. ap. HEGI 1924 syn. pro var. alpestre Guss.
- nevadense (Boiss.) Coombe — BOISSIER pro sp. ap. COOMBE 1968 pro ssp.,
 BURDON 1983 idem
- nigrescens Schur non Viv. et al — SCHUR 1866 pro sp., ap. MANSFELD 1959,
 1986, syn. pro T. repens L., SIMONKAI 1866 idem, DUKE 1981 idem
- nigricans Schur non al. — SCHUR 1866 pro sp., ap. A. NYÁRÁDY 1957 syn. pro
 f. gracillimum (Schur) Nyár.
- nomophyllum h.l. — supraconvar. nova
- obcordatum E. I. Nyár. — E.I. NYÁRÁDY 1942 pro ssp., ap. A. NYÁRÁDY pro
 var., CSÚRÖS et RESMERIJA 1973, idem

Table 1 (cont.)

- occidentale Coombe — COOMBE 1961 ap. COOMBE 1968 pro sp., BURDON 1983 pro ssp.
- ochranthum Maly ap. E.I. Nyár. — MALY 1900 pro sp., ap. ASCHERSON et GRAEBNER 1907 idem, syn pro T. transsilvanicum Schur, T. pallescens auct. non Schreb., E.I. NYÁRÁDY 1940 pro ssp. in Flora Exsiccata Romaniae (lectotypus), A. NYÁRÁDY 1957 pro var., JULEN 1959 idem, COOMBE 1968 pro ssp., BOROS et SZABÓ 1968 sec. A. et G., SOÓ 1970 idem, CSÚRÖS et RESMERIJA 1973 pro var., BELDIE 1977 pro ssp., BURDON 1983 idem, GILLET 1985 idem
- ochroleucum Thell. — THELLUNG 1914 pro var., ap. HEGI 1924 pro f. in var. typicum, SOÓ 1966 pro l., BOROS et SZABÓ 1968 pro f. culta.
- orbelicum Vel. — VELENOVSKI 1889, 1891 pro sp., ap. SOÓ 1966 pro ssp. cf. PAWLOWSKI 1949, COOMBE 1968 idem, KOZUHAROV 1976 idem, syn. pro var. orbelicum (Vel.) Stoj. et Stef. et pro var. ochranthum Maly ap. Achers. et Graebn., BELDIE 1977 pro ssp., BURDON 1983 idem, GILLET 1985 idem
- orphanideum Boiss. — BOISSIER 1856 pro sp., HEGI 1924 pro var. syn. var. pseudo-elegans Gib. et Bel., JÁVORKA 1925 pro ssp., BORZA 1949 idem, A. NYÁRÁDY 1957 pro var. syn. T. caespitosum Schur non al., JULEN 1959 idem syn. var. alpinus Schur, BELDIE 1972 pro var., COOMBE 1968 pro ssp., BOROS et SZABÓ 1968 idem, CSÚRÖS et RESMERIJA 1973 pro var., BURDON 1983 pro ssp.
- pallescens auct. non Schreb. — BELDIE 1977, syn. pro ssp. ochranthum (Maly.) Nyár. (!?)
- pentaphyllum hort. — A. NYÁRÁDY 1957 pro monstr., SOÓ 1966 pro l., BOROS et SZABÓ 1968 pro f.
- perenne h.l. — provar. nova
- phyllanthum Ser. — SERINGE 1815 ap. A.P. DE CANDOLLE 1825, HEGI 1924 pro f. syn. T. umbellatum Losc. et f. monstruosum Gaud., TURKINGTON et al. 1983 pro f. cf. FIORI et BEGGER 1929
- polyphyllum sa.a. erroneo polyphylla — TABERNAEMONTANUS, ap. HEGI 1924 por f., syn. f. pentaphyllum et f. tetraphyllum
- praecox h.l. — provar. nova
- proliferum Plusk. — PLUSKAL ap. HEGI 1924 pro f.
- prolificum h.l. — provar. nova
- prostratum Biasol. non DC. et Lam. — BIASOLETTI pro sp., ap. HEGI 1924 syn. pro var. alpestre Guss., syn. biasolettii (Steud. et Hochst.) A. et G., syn. T. biasolettianum Steud. et Hochst., syn. T. neglectum Noe, syn. T. monvernense Shuttlew. (?)
- prostratum DC. et Lam. non Biasol. — A.P. DE CANDOLE et LAMARCK 1805 pro var., ap. HEGI 1924, syn. pro f. microphyllum Lagr.-Foss., syn. var. minus Gib. et Bel.
- prostratum Nym. — NYMAN 1878 pro sp., ap. COOMBE 1968 pro ssp. syn. T. biasolettii Steud. et Hochst., EHRENDORFER et al. 1973 idem, BELDIE 1977 idem, BURDON 1983 idem, GILLET 1985 idem
- prostratum-minimum Porc. — PORCIUS 1878 pro var. (?) ap. SIMONKAI 1886 syn. T. galerosum (glareosum?) Schleich. et T. pallescens Schreb.
- prostratum Schur — SCHUR 1866 pro var. ap. A. NYÁRÁDY 1957 syn. pro f. microphyllum (Lagr.-Foss.), SOÓ 1966 syn. pro f. gracillimum Schur
- pseudo-elegans Gib. et Bel. — GIBARDI et BELLELLI ap. HEGI 1924 syn. pro var. orphanideum Boiss.
- pseudopallescens J. Murr — J. MURR 1923 ap. SOÓ 1966 pro l.
- pubescens Peterm. — PETERMANN 1846 pro sp., ap. SOÓ 1966 pro f., BOROS et SZABÓ 1968 idem.
- reflexum Benkő — BENKŐ 1778 pro sp. ap. SIMONKAI 1886 syn. pro T. repens

Table 1 (cont.)

<u>repens</u> L. — LINNÉ 1753 pro sp. ap. gen. auct. <u>On infraspecific levels</u> : A.P. DE CANDOLLE 1825 pro (var.) <u>alfa</u> , A. NYÁRÁDY 1957 var. <u>typicum</u> et f. <u>genuinum</u> !, SOÓ 1966 pro f., syn. f. <u>sylvestre</u> Alfe. et f. <u>genuinum</u> A. et G., COOMBE 1968 pro ssp., BOROS et SZABÓ 1968 idem syn. ssp. <u>typicum</u> A. et G. incl. f. <u>repens</u> syn. f. <u>sylvestre</u> Alef. et f. <u>genuinum</u> A. et G., EHRENDORFER et al. 1973 idem, KOZUHAROV 1976 pro ssp. et var., BELDIE 1977 pro ssp., BURDON 1983 idem, CLEVELAND 1985 pro sp. et var.
<u>roseum</u> Peterm. — PETERMANN 1846 ap. HEGI 1924 pro f., SOÓ 1968 pro l., BOROS et SZABÓ 1968 pro f. <u>culta</u>
<u>rubescens</u> Ser. — SERINGE ap. A.P. DE CANDOLLE 1825 pro (var.) <u>beta</u> , BURDON 1983 pro var.
<u>striatum</u> Priszter — PRISZTER 1966 pro f. ap. SÓO 1966 pro l.
<u>sylvestre</u> (<u>silvestre</u>) Alfe. non al. — ALEFELD 1866 pro f. (var.), ap. HEGI 1924 pro div. f. spont., JULEN 1959 pro var.
<u>sylvestre</u> Erith — ERITH 1921 syn. var. <u>typicus</u> f. <u>sylvestre</u> ZEVEN et ZHUKOVSKY pro var. spont. div., S.U.K. 1977 pro f., VACEK et al. 1979, 1982 idem, BURDON 1983 syn. pro ssp. et var. <u>repens</u>
<u>tetraphyllum</u> hort. — HEGI 1924 pro f., A. NYÁRÁDY 1957 pro monstr., SOÓ 1966 pro l., BOROS et SZABÓ 1968 pro f.
<u>townsendii</u> Beeby — BEEBY ex LOUSLEY 1971 ap. BURDON 1983 pro ssp. <u>prostratum</u> Nyman var. <u>townsendii</u>
<u>transsilvanicum</u> Schur — SCHUR 1866 pro sp., ap. A. NYÁRÁDY 1957 pro var., CSÜRÖS et RESMERIJA 1973 idem, BELDIE 1977 syn. pro ssp. <u>ochranthum</u> (Maly) E.I. Nyár.
<u>typicum</u> A. et G. — ASCHERSON et GRAEBNER 1907 pro var., HEGI 1924 idem, A. NYÁRÁDY 1957 idem, CSÜRÖS et RESMERIJA 1973 idem, S.U.K. 1977 pro f.
<u>uliginosum</u> Schur — SCHUR 1877 ap. SOÓ 1966 pro f.
<u>ungiculatum</u> Ser. — SERINGE ap. A.P. DE CANDOLLE 1825 pro (var.)
<u>umbellatum</u> Losc. — in HEGI 1924 syn. f. <u>phyllanthum</u> Ser.
<u>virescens</u> s.a. — ex Herbarium Haussknecht

The evolutionary divergence of cultivated *Trifolium repens* during the last three centuries due to selection and later to breeding, as reflected in the names of the different cultivar groups is presented in Table 2.

Based on these findings, on the data collected from herbaria, nature and experimental fields, a classification is proposed for the consistent grouping of wild and cultivated white clover (Table 3). Latin diagnoses have been also attached for the proposed new taxa. Voucher specimens have been prepared, too.

The primary white clover gene pool (GP-1) seems to consist of 8 spontaneous subspecies and 4 major cultivated variety groups considered as convarieties. There is an easy crossability and gene flow among the members of this pool.

Table 2

Variability — and microevolution — in cultivated white clover (*Trifolium repens* L.) reflected by names assigned to different cultivar groups in last 300 years

Year	Name of cult. group	Source	Notes
1578	<i>Trifolium</i> (album)	MELIUS	first mentioned in Hungarian botany
1651	luxurians	BAUHIN	in Switzerland?
1753	<i>Trifolium repens</i>	LINNAEUS	botanical name valid
1846	— grandiflorum	PETERMANN	culta?
1847	— giganteum	LAGREZE-FOSSAT	culta?
1896	— macrocephalum	FIORI, PAOLETTI	N. Italy, var.
1907	— cultum	ALEFELD	Germany, f.
1921	— hollandicum	ERITH	The Netherlands?
1924	— atropurpureum		culta, f.
	— ladino	HEGI	culta, f.
	— lodi, lodigense		culta, f.
1936	— giganteum	RAPAICS	culta, f., Hungary
1957	— giganteum	NYÁRÁDY	f. culta, Romania
	— hollandicum		
1959	— giganteum		
	— hollandicum	JULEN	f. culta, Europe
	— sylvestre		
1966	— small, medium 1, medium 2, large leaved	SPEEDING et al. 1972 ap., anonym. source, 1966	f. culta, England
1968	— hollandicum, giganteum	JÁNOSSY	f. culta, Hungary
1969	— lodi et repens	MÉM-Sz.	f. culta, Hungary
1972	— (not named)	Bundessorten-liste	no diff. types in Germany (?)
1975	— nain (sauvage)		
	— hollandicum	INRA	f. cult., France
	— ladino (geant)		
1976	— nanum (wild)	EVANS	f. culta, England
	— hollandicum		
1977	— sylvestre	S.U.K.	f. culta, European Socialist Countries
	— hollandicum		
	— giganteum		
1979	idem	VACEK et al.	cultivar types, CSSR
1980	idem	SZABÓ	cultivar types, Romania
1980	— nano	ANONYMOUS (Reg. var.)	cultivar groups, Italy
	— comune		
	— ladino		
	— ladino gigante		
1981	— small leaved	DUKE	cultivar types, USA and world
	— intermediate		
	— large leaved		
1983	— witte cultur-	SNEEP et al.	cultivar groups, the Netherlands
	— witte weide-		
	— grodبلادige-		

Table 2 (cont.)

Year	Name of cult. group	Source	Notes
1983	— sylvestre		
	— cultum		
	— giganteum (lodigense)	BÁNYAI	cult. groups, Hungary
1985	— small leaved (wild)	GIBSON et	cult. groups, USA
	— intermediate	COOPE in	
	— common	TAYLOR (Ed.)	
	— large		

The secondary white clover gene pool (GP-2) contains at present four species successfully crossed in hybridization experiments with *Trifolium repens* L. These are *T. uniflorum* L., *T. nigrescens* Viv., *T. isthmocarpum* Brot. and *T. ambiguum* Bieb. Another species — *T. occidentale* Coombe — was considered here as a subspecies and was included in the primary gene pool. It is worth to note, that this is a case when taxonomic treatment deeply influence the interpretation of genetic results and crossing experiments, too.

The tertiary gene pool (GP-3) consists of different *Trifolium* species, some of them still seems to be linked to white clover gene pool by intermediate species common on secondary level e.g. *T. montanum* and *T. hybridum* both by *T. ambiguum*; *T. xerocephalum* by *T. nigrescens*.

A "quaternary" gene pool (GP-4) comprising other members of the *Fabaceae* family is also conceivable, taking into account the different vector organisms common for the *Fabaceae* (e.g. the different *Rhizobium* and *Mycoplasma* species).

Almost every subspecies or (con)varietas may have, in different ecological conditions, parallel variations due partly to accumulation of similar genes (allels) and to the phenotypic plasticity of the species. These may be regarded taxonomically — if useful — as *lusus* or as parallel forms in a sense indicated by VAVILOV (1951). Such parallel forms (pf.) are for example pf. *longipes* (Peterm.), pf. *microphyllum* (Lagr.-Foss.), pf. *minus* (G. et B.), pf. *pubescens* (Peterm.), pf. *roseum* (Peterm.), pf. *rubescens* (Peterm.), pf. *uliginosum* (Schur) etc.

Beside that, a series of teratological forms have been defined nomenclaturally; forms which are caused frequently by microorganisms — mostly by mycoplasmas — on different organs of the white clover plant. Such

Table 3

Taxonomic units — proposed also as OZU's — for grouping white clover germplasm

Genus: Trifolium L.
 Subgenus: Trifoliastrum Ser.
 Sectio: Armoria Presl
 Subsectio: (Eu)Armoria Gib. et Bel.
 Species: Trifolium repens L.

Spontaneous variabilityCultivar groups

ssp. <u>nevadense</u> (Boiss.) Coombe	supraconvar. <u>nomophyllum</u> h. l.
ssp. <u>occidentale</u> (Coombe) Burdon	convar. <u>giganteum</u> (Lagr.-Foss.) em. h. l.
ssp. <u>ochranthum</u> (Maly) E.I. Nyár.	provar. <u>bienne</u> h. l.
var. <u>ochranthum</u>	
var. <u>transsilvanicum</u> (Schur)	provar. <u>perenne</u> h. l.
ssp. <u>orbelicum</u> (Vel.) Pawl.	
var. <u>orbelicum</u>	convar. <u>hollandicum</u> (Erith) em. h.l.
var. <u>obcordatum</u> E.I. Nyár.	
var. <u>helveticum</u> Scheele	provar. <u>praecox</u> h.l.
ssp. <u>orphanideum</u> Boiss.	provar. <u>prolificum</u> h.l.
ssp. <u>prostratum</u> Nyman	convar. <u>nanum</u> h.l.
var. <u>prostratum</u>	
var. <u>townsendii</u> Beeby	convar. <u>arcto-alpinum</u> h. l.
ssp. <u>repens</u>	
var. <u>repens</u>	
var. <u>sylvestre</u> Alef.	
var. <u>fissurae</u> h.l., prov.	
var. <u>arcticum</u> h.l., prov.	
ssp. <u>grandiflorum</u> (Peterm.) h.l.	

teratoforms (tf.) or monstruosities have been described first under the names monstruosum by F. ZIMMERMAN, phyllanthum by SERINGE, polyphyllum by PLUSKAL, ungiculatum by SERINGE, umbellatum by LOSE, vorescens (s.a.) etc. The f. striatum Priszter could perhaps be genetically defined, but striate leaves emerge due to virus infections, too.

Addenda ITrifolium repens L. — Diagnoses novae taxonum cultivatorum

Supraconvar. (ssp.) nomophilum supraconvar. nova — populationes cultae ab animalibus hominibusque calcatorum praediorum, e.g. pascuis, locis graminosis. Semina dura infra 20 pro cento.

Convar. nanum em. hoc loco, convar. nova — foliolis elliptico-obcordatis, parvis, longitudine infra 15 mm, stolonibus tenuibus circiter 1,5 mm in diam., ramificatis, pluribus radicibus adventivis praeditis; cultivar typica pro convar.: cv. "S-184".

Convar. arcto-alpinum convar. nova — foliolis obcordatis 20–25 mm longis, parte superiora manifeste dilatata, saepe — sine macula foliare. Seminationis primo anno pauperculo modo florescit. Greges cultivarietatum septentrionalum includens et ad condiciones alpinas Europae Centralis accommodatae. Cultivar typica pro convar.: Cv. "Nora".

Convar. hollandicum (Erith) em. hoc loco — foliolis obcordato-ellipticis, 25–35 mm longis, stolonibus circiter 2 mm diametro crassi, longis, — ramificatis. Cultovarietates in Europa occidentali natas prope regionem Mari Septentrionali includentes. Cultivar typica pro convar.: cv. "Milkanova".

Provar. praecox provar. nova — cultivarietates praecoces; convar. hollandicum pertinens. Typus generativus jam primo anno abundiflorus. Inflorescentiae pedunculus vulgo 1,5 — 2-ies petioli longitudinem in altitudine superans. Cultivar typica pro provar.: cv. "Georgicon-66".

Provar. prolificum provar. nova, syn. provar. hollandicum sensu stricto — tardivorum cultivarorum grex; convar. hollandicum pertinens. Typo vegetativo. Pedunculus longitudinem petioli vulgo non ultra 1,5-ies superans, vel brevior. Cultivar typica pro provar.: cv. "Milkanova".

Convar. giganteum (Lagr.-Foss.) em. hoc loco — foliolis magnis maximis, longitudine ultra 35 mm. Stolonibus crassis, ultra 33 mm diam., viridescentibus, vulgo lentier ramificatis; radicibus adventivis solum ad foliorum insertionis instructis, rarioris. Inflorescentia magna, plus quam 45–50 flores. Cultivatorum greges ex Italia septentrionale provenientes. Cultivar typica pro convar.: cv. "Regal".

Provar. bienne provar. nova; convar. giganteum pertinens — foliolis magnis, obcordatis, macula foliolorum 100 pro cento manifesta. Perennitas plantae deminuta. Cultivar typica pro provar.: cv. "Tamar".

Provar. perenne provar. nova; convar. giganteum pertinens; syn. convar. giganteum sensu stricto — foliolis magnis, lato obcordatis. Macula foliare varia. Perennitas plantae ultrae 4 annorum.

Cultivar typica pro provar.: Cv. "Regal".

Addenda II

Species, subspecies, variety and convariety names for white clover —
Trifolium repens L.

SPECIES NAMES (invalid names, except T. repens L.)

- Trifolium alpinum Schur, non L. = ssp. alpinum (Schur) Rothm.,
 BELDIE 1977
T. anomalum Schrank 1819, MANSFELD 1959
T. angustifolium Krösche 1924, SOÓ 1966
T. biasolettii St. et Hoechst. = ssp. prostratum Nym.
T. caespitosum Schur 1866, A. NYÁRÁDY 1957
T. Galerosum Schur, non Schleich. (1866), A. NYÁRÁDY 1957
T. helveticum Scheele 1843, HEGI 1924
T. limonium Phil. 1856, MANSFELD 1959
T. neglectum Noe ap HEGI 1924, SOÓ 1966
T. monvernense Shutlew. ap, SOÓ 1966
T. nigrescens Schur 1866, non Viv., A. NYÁRÁDY 1957
T. orbelicum Vel. 1889, SOÓ 1966
T. orphanideum Boiss. 1856, A. NYÁRÁDY 1957
T. orphanideum auct., non Boiss. MANSFELD 1959, GELDIE 1977
T. pallescens auct., non Schreb.
T. prostratum Schur 1866, SOÓ 1966
T. repens L. 1753
T. transsilvanicum Schur 1866, A. NYÁRÁDY 1957
T. umbellatum Losc. = monstr., HEGI 1924

SUBSPECIES NAMES

- ssp. nevadense (Boiss.) D. E. Combe 1968, COMBE 1968
 ssp. occidentale (Coombe) Burdon, BURDON 1983
 ssp. ochranthum E. I. Nyár. 1940, D. E. COMBE 1968, BELDIE 1977 sub
 ssp. ochranthum (Maly) Nyár.
 ssp. orbelicum (Velen.) Pawl. 1949, SOÓ 1966, D. E. COMBE 1968,
 BELDIE 1977
 ssp. orphanideum (Boiss.) Jáv. 1924, SOÓ 1966, D. E. COMBE 1968
 ssp. prostratum Nyman 1878, COMBE 1968, EHRENDORFER et al. 1973 =
T. biasolettii St. et Hoechst.
 ssp. repens, SOÓ 1966, D. E. COMBE 1968, EHRENDORFER et al. 1973,
 BELDIE 1977

SOME SPONTANEOUS VARIETY NAMES

- var. alpestre Gussone syn. p.p. var. biasolettii (St. et H.) A. et
 G., SOÓ 1966 = T. prostratum Nym (?), T. biasolettianum St. et
 H. (!), T. neglectum Noe, T. monvernense Shutlew., cf. HEGI
 1924.
 var. alpinum Schur = var. orphanideum Boiss. (?), HEGI 1924
 var. biasoletti (!) sine auct. et an. (s. a. a.), JULEN 1959
 var. obcordatum Nyár. 1942 = T. galerosum Grec. 1909, non Schleich,
 A. NYÁRÁDY 1957
 var. ochranthum Maly in A. et G. 1907, A. NYÁRÁDY 1957, JULEN 1959

- var. orphanideum Boiss. 1872 = var. alpinum Schur, A. NYÁRÁDY 1957, JULEN 1959
- var. giganteum s. a. a., = Lodi, Ladino clover, ZEVEN et ZHUKOVSKY 1975
- var. minus auct. = var. prostratum
- var. macrocephalum auct.
- var. prostratum DC. et Lam., non Biasol. = var. minus Gib., f. microphyllum Lagr.-Fossat 1847, HEGI 1924
- var. sylvestre Erith 1924 (?) = var. typicum syn. var. genuinum auct., A. NYÁRÁDY 1957, JULEN 1959, ZEVEN et ZHUKOVSKY 1975 (wild type)
- var. repens = var. typicum p.p.
- var. typicum A. et G. 1907 = var. sylvestre p. p. var. repens, A. NYÁRÁDY 1957, JULEN 1959

SOME FORM NAMES (spontaneous and cultivated)

- f. alloideum Dorc. s. a., TURKINGTON and BURDON 1983
- f. atropurpureum hort., HEGI 1924
- f. caespitosum Domin 1932, SOÓ 1966
- f. cultum Alef. 1866, p. p. = f. giganteum Lagr.-Fossat = f. macrocephalum Fiori et Paol. (an vero?), HEGI 1924, VACEK 1982
- f. foliatum Rigo 1883 = f. terat.
- f. genuinum A. et G. = f. sylvestre, HEGI 1924, A. NYÁRÁDY 1957
- f. giganteum Lagr.-Fossat 1847 = f. cultum Alef. p. p. = macrocephalum Fiori et Paol., = f. lodigense hort., HEGI 1924, A. NYÁRÁDY 1957, JULEN 1959, SOÓ 1966, VACEK et al. 1979 (pro tipus)
- f. grandiflorum Peterman 1846, HEGI 1924, A. NYÁRÁDY 1957, SOÓ 1966
- f. gracillimum (Schur 1866 syn. pro f. prostrato Schur!) A. Nyár. 1957 = f. minus Baldacci in Rohlena 1911, A. NYÁRÁDY 1957, SOÓ 1966
- f. hollandicum Erith ex Jáv. et Soó 1951, hort., A. NYÁRÁDY 1957, JULEN 1959, SOÓ 1966, VACEK et al. 1979
- f. ladino s. a., BARCHIKOWSKA 1976. ap. VACEK et al. 1982
- f. lodigense hort. = f. giganteum (Lagr.-Fossat) Soó, HEGI 1924, A. NYÁRÁDY 1957, SOÓ 1966
- f. longipes Peterman 1846, HEGI 1924, SOÓ 1966
- f. luxurians DC. in herb, A. et P. de CANDOLLE 1825 cf. C. BAUHNUS 1574 (!)
- f. macrocephalum Fiori et Paol. = f. giganteum, HEGI 1924
- f. microphyllum Lagr.-Fossat 1847 = var. prostratum DC. et Lam. non Biasol., var. minus Gib. et Belli, HEGI 1924, A. NYÁRÁDY 1957
- f. monstruosum Fr. Zimm. = f. pentaphyllum, HEGI 1924
- f. minus Baldacci in Rohlena 1911 = f. gracillimum (Schur.) A. Nyár., SOÓ 1966
- f. pentaphyllum hort., HEGI 1924
- f. prostratum Schur 1866 = f. microphyllum Lagr.-Fossat, HEGI 1924
- f. phyllanthum Ser. = f. proliferum Pluskal = f. monstruosum Fr. Zimm., idem Gaudin, T. umbellatum Losc., HEGI 1924, SOÓ 1966 TURKINGTON et BURDON 1982 (f. phyllanthum (Ser.) Fior. et Beg.), cf. monstr. f. phyllanthum DC!
- f. repens, A. et P. de Candolle 1825, SOÓ 1966 (syn. f. sylvestre Alef. (?), f. genuinum A. et G., p. p.)
- f. roseum Petterm., HEGI 1924

- f. rubescens Ser. in mns., P. et A. DE CANDOLLE 1825
- f. silvestre (silvestre) Alef 1866 = f. repens (?) cf. JULEN 1959
sine cat. tax. cit. ERITH 1924!), = f. typicum A. et G., SOÓ 1966, et auct. div.
- f. tetraphyllum hort., HEGI 1924
- f. uliginosum Schur 1877, SOÓ 1966
- f. virescens s. a. a., BORNMÜLLER 1903 in Herb. Hausknecht (cf. monstr.)

SOME LUSUS NAMES (1.)

- 1. atropurpureum hort., SOÓ 1966
- 1. angustiflorum (Krösche 1924 p. sp.) Soó 1946, SOÓ 1966
- 1. ochroleucum Thell. 1914, SOÓ 1966
- 1. pentaphyllum hort., SOÓ 1966
- 1. pseudopallescens J. Murr. 1923, SOÓ 1966
- 1. roseum Peterm. 1846, SOÓ 1966
- 1. striatum Priszter 1966, SOÓ 1966
- 1. tetraphyllum hort., SOÓ 1966

MONSTRUOSITY NAMES (including teratologies caused by mycoplasma)

- m. anomalum Schreb = m. phyllanthum auct., HAUSER 1884, 1891, LOHMEYER s. a., RIGO 1893 in Herbario Hausknechtii
- m. (f.) foliatum Rigo 1883, in Herbario Hausknechtii
- m. monstruosum Gau 1829, SOÓ 1966
- m. (f.) monstruosum Fr. Zimm., non Gaud = f. phyllanthum Ser, f. proliferum Pluskal, auct. div. in Herbario Hausknechtii
- m. monstruosa s. a. in herb., auct. div (TUCKENHEIM 1871, ZABEL 1910, FRITSCH 1890, MATTHIAS 1900) in Herbario Hausknechtii
- m. pentaphyllum hort., A. NYÁRÁDY 1957
- m. (f.) phyllanthum (Ser. in mns.) DC. 1825 cf. P. et A. DE CANDOLLE 1825 et in Herbario Hausknechtii (RIGO 1893, COPINEAU 1891, BARTH 1908) syn. m. anomalum p. p.
- m. proliferum Pluskal s. a. = f. phyllanthum Ser., f. monstruosum Fr. Zim., non Gaud.
- m. tetraphyllum hort., A. NYÁRÁDY 1957
- m. ungiculatum (Ser. in mns.) DC., A. et P. DE CANDOLLE 1825
- m. virescens s. a., in Herbario Hausknechtii (WISRGEN 1898, FLOSSER 1905, KOPPE 1917, MEYER 1961)

CULTIVAR GROUP NAMES (in different countries)

- France: Botanical types: 1. Ladino (geant), 2. hollandicum (intermediaire), 3. sauvage (nain). Source: INRA, 1975.
- Great Britain: Types or cultivar groups: 1. large leaved (Ladino), 2. medium leaved (1), 3. medium leaved (2), 4. small leaved, 5. wild populations. Sources: DAVIES 1967, SACKVILLE-HAMILTON 1979, SPEDDING et al. 1972.
- Hungary: Types (subspecies). 1. white clover, 3. Lódi clover. Source: MÉMSZ 69/1, 1979.
- Italy: Gruppi (tipi): 1. Ladino Gigante, 2. Ladino, 3. Comune, 4. Nano. Source: REG. VAR. ITALIANO 1980.
- Romania: Tipuri: 1. giganteum (Ladino), 2. hollandicum (intermediar), 3. silvestre (marunt). Sources: MOGA et al. 1983, PUJA et al. 1980, SZABÓ 1980.

Switzerland: Typ: 1. Wilde Typ, 2. Mähwiese Typ. Source: KREBS s. a.
The Netherlands: Types: 1. Good bladige witte klaver (voor stoppelgewas),
2. Witte weideklaver, 3. Witte cultuurklaver. Source: SEEP et al.
1983.

U.S.A. Type: Ladino, Gigant. Source: Farmers Leaflet, 1966.

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REFERENCES

- Alefeld, F. (1866): Landwirtschaftliche Flora. Berlin.
- Ascherson, P., Graebner, P. (1907): Synopsis der mitteleuropaischen Flora. Leipzig, VI/2.
- Bányai, L. (1983): *Trifolium repens* L. In: Bánai L. (ed.), Production of papilionaceous crops. (In Hungarian). Budapest.
- Beldie, A. (1977): Flora României. București.
- Bonstedt, C. (1931): Pareys Blumengartnerei. I. Berlin.
- Boros, A., Szabó, L. (1968): The taxonomy of clover species. In: Jánossy, A. et al. (ed.), Production and selection of clovers (In Hungarian). Budapest.
- Burdon, J.J. (1985): Biological Flora of the British Isles. No. 154. *Trifolium repens* L. Journ. of Ecol. 71: 307-330.
- Cleveland, R.W. (1985): Reproductive Cycle and Cytogenetics. In: Taylor, N. (ed.), Clover Science and Technology. Agr. Sci. Ser. 45, Madison.
- Coombe, D.E. (1968): *Trifolium*. In: TUTIN, G. et al. Flora Europaea. II. 157-172. Cambridge.
- Csűrös, S., Resmerița, I. (1973): *Trifolium repens* L. In: Resmerița I. et al., Monografia trifoiului din Romania. București.
- Daday, H. (1958): Gene frequencies in wild populations of *Trifolium repens* L. III. World distribution. Heredity 12: 169-184.
- Davies, W.E., Young, N.R. (1967): The Characterisation of European, Mediterranean and other populations of white clover (*Trifolium repens* L.). Euphytica 16: 330-340.
- Dostál, J. (1982): Seznam cévnatých rostlin kvetený Československé. Praha.
- Duke, J. (1981): Legumes of World Economic Importance. Oxford.
- Ehrendorfer, F. (ed.) (1973): Liste der Gefäßpflanzen Mittel-Europas. 2. Aufl. Stuttgart.

- Evans, A.M. (1976): Clovers. *Trifolium* spp. In: Simmonds, N.W. (ed.). Evolution of Crop Plants. London-New York.
- Gibson, P.B., Coope, W.A. (1985): White clover. In: Taylor op. cit. cf. Cleveland.
- Gillet, J.M. (1985). Taxonomy and morphology. In: Taylor op. cit. cf. Cleveland.
- Harlan, J.R., De Wet, J.M.J. (1971): Toward a rational classification of cultivated plants. Taxon 20: 509-514.
- Hegi, G. (1923, 1924): Illustrierte Flora von Mitteleuropa. IV. 3: 1302-1305. München.
- Heywood, V.H. (1959): The taxonomic treatment of ecotypic variation. Syst. Ass. Publ. London. 3: 87-112.
- Janchen, E. (1957): Catalogus Florae Austriae. I/2. Wien.
- Jánossy, A. (1966): Clovers. In: Láng G. (ed.) Manual of plant production. (In Hungarian). Budapest.
- Josifović, M. (ed.) (1972): Flore de la Republique Socialiste de Serbie. 4. Beograd.
- Julen, G. (1959): Weissklee. *Trifolium repens* L. In: Kappert, H., Rudolf, W. (ed.) Handbuch der Pflanzenzüchtung. IV. Berlin-Hamburg.
- Kozuharov, S. (1976): *Trifolium* L. In: Flora Reipublicae Popularis Bulgari- cae, 6: 325-338. Sofia.
- Linnaeus, C. (1753): Species plantarum. Stockholm.
- Mansfeld, R. (1959): Vorläufiges Verzeichnis landwirtschaftlich oder gärt- nerisch kultivierter Pflanzenarten. Kulturpflanze. Beiheft. 2. Ber- lin. Neuauflage Ed. by J. Schultze-Motel, 1986, Berlin-Stuttgart.
- Nyárády, A. (1957): *Trifolium* L. In: Flora Republici Populare Romîne. V: 151-222. Bucureşti.
- Rapaics, R. (1936): The four leaved white clover. (In Hungarian). Pótfüze- tek. Term. Tud. Közl. 67: 136-137.
- Schultze-Motel, J. (ed.) (1986): Rudolf Mansfeld's Verzeichniss... cf. Mansfeld, R.
- Seringe, N.Ch. (1825): Leguminosae. In: A.P. De Candolle, Prodromus ... Regni Vegetabilis ... 2; 171-215; 354-380. Paris.
- Simonkai, L. (1886): An improved survey of the vascular flora of Trans- sylvania. (In Hungarian). Budapest.
- Sneep, J., Van der Zaag, E.D., Vos, M. (1983): Beschrijvende Rassenlijst voor Landouwegewassen. Wageningen.
- Soó, R. (1966): Synopsis systematico-geobotanica florae vegetationsique Hungariae, 2: 330-322. Budapest.
- Spedding, R.C.W., Diekmans, E.C. (ed.) (1972): Grasses and Legumes. Brit. Agr. Bull. 49. Oxford.
- Szabó, T.A. (1978): Melius Péter - Herbarium, Colosvár 1578. Bukarest.
- Szabó, T.A. (1980): Phenotypic variability in white clover (*Trifolium repens* L.) in Romania. Bul. Inst. Agr. Cluj. Ser. agr. 34: 35-42. (In Roumanian).

- Szabó, T.A. (1983): Applied biology in the evolution of cultivated plants. (In Hungarian). Bukarest.
- Taylor, N.L. (1986): Chromosome numbers of *Trifolium* species from Roumania. Not. bot. hort. agrobot. Cluj. 16.
- Thiemann, H. (1980): Fertilitätsverhältnisse bei hexaploidem Weissklee (*Trifolium repens* L.). Biol. Rundsch. 18: 40-43.
- Vaček, V., Blahout, J. (1979): Ideotyp jetele plaziveho (*Trifolium repens* L.) do roku 2000. Sbor CSAZ. 34: 213-220.
- Vavilov, N.I. (1951): The origin, variation, immunity and breeding of cultivated plants. Chronica Botanica 13.
- Zeven, A.C., Zhukovsky, P.M. (1975): Dictionary of Cultivated Plants and their Centres of Diversity. Wageningen.
- x x x (1969). Small seed legumes. Production for the varietal certification. MEM - Sz. 69. Budapest.
- x x x (1972): Beschreibende Soertenliste für Gräser und landwirtschaftliche Leguminosen. Hannover.
- x x x (1975): Bulletin des variétés. Plantes fourrageres. Versailles.
- x x x (1977): Shirokiy unifitsirovanniy klassifikator roda Trifolium L. Piestani. (Abbrev.: S.U.K. 1977)
- x x x (1979): Aspetti della caratterizzazione varietale in trifoglio bianco. Sementi elette 24, 6: 18-22.
- x x x (1980): Registre Varietale Italiana. Lodi.

XYLOTOMICAL EXAMINATIONS OF SOME VENEZUELAN TREE SPECIES (CAESALPINIACEAE I)

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This paper is a continuation of the dissertation "Xylotomic examinations of some Venezuelan species" started in 1981.

The authors make known the exterior morphological and ecological characteristics, the habitat and the main anatomical features of the xylem for four Venezuelan species of Caesalpinaceae, namely: Caesalpinia coriaria (Jacq.) Willd., Caesalpinia mollis (H.B. et K.) Spreng., Caesalpinia pulcherrima (L.) Sw. and Cassia reticulata Willd.

MATERIAL AND METHOD

The blocks made from the wood of the four species were softened in a mixture of water and glycerin, in BRINZER's autoclave at 1.5-2.0 atm., then transversal, tangential and radial sections were made. The sections were stained with an alcoholic solution of Toluidin-blue. The maceration of tissues was made with the SCHULZE method (SÁRKÁNY-SZALAI 1964).

Length of fibres and vessel elements, tangential and radial diameters of vessels, width and height of medullary rays and other characteristics were determined from 50-100 measurements. Enlarged microphotographs were made of each section.

External morphology and distribution on the basis of descriptions by Prof. L.J.C. Cumana.

EXTERNAL MORPHOLOGY

Caesalpinia coriaria (Jacq.) Willd.

Shrub or small tree 3-7 m high, foliage deciduous, unarmed; stem short and crooked; branches horizontally extended. Leaves alternate, bipinnately compound; pinnae 3-9 pairs; leaflets 12-28 pairs, 3-9 mm long, 1-2 mm wide, rounded apically, asymmetrical basally, linear-oblong, pubescent on both surfaces, conspicuously dotted below. Panicle bent, axillary or

terminal with numerous white-yellowish flowers. Sepals 5, imbricated, 3-4 mm long, the exterior of bigger size. Petals 5, imbricated, 3.5-4 mm long. Stamens 10 of different size, 4-6.5 mm long; filaments conspicuously pilose towards the base; anthers longitudinally dehiscent; connective somewhat prominent. Gynoecium 7.5-9 mm long, curved, inserted into the base of a hollow receptacle. Legume glabrous, lustrous, curved or S-shaped, 3-6 cm long, 1-2 cm wide.

Autochthonous species known as "Dividive", "Guatapanare"; grows in arid regions, in xerophilous forests, mainly in the Coastal Range of Mountains. Rich in tannins and colouring substances.

Caesalpinia mollis (H.B. et K.) Spreng.

Shrub or small tree 3-5 m high, unarmed, foliage deciduous. Leaves alternate, bipinnately compound; pinnae 3-4 pairs; leaflets 7-8 pairs, pubescent on both surfaces 3.4-5 cm long, 1.5-1.8 cm wide, oblong-lanceolate, acute apically, cuneate basally. Inflorescence of terminal or axillary racemes with 10-20 yellow flowers. Sepals 5, imbricated, 8-10 mm long, 2-4 mm wide; petal exterior of larger size, very conspicuous with a laciniate margin. Petals 5, imbricated, 9-12 mm long, 4-8 mm wide. Stamens 10, 5-6 mm long, 4 of them larger; filaments hairy towards the base; anthers longitudinally dehiscent. Gynoecium 9-10 mm long, pubescent, slightly curved, inserted into the bottom of a hollow receptacle. Legume chartaceous, pubescent, 10-15 cm long, 3-4 cm wide.

Autochthonous species known as "Acacia"; frequent in xerophilous and trophophyll forests; sometimes cultivated as an ornamental.

Caesalpinia pulcherrima (L.) Sw.

Shrub, 2-4 m high, fragrant, spiny. Leaves alternate, bipinnately compound, glabrous; pinnae 5-10 pairs; leaflets 8-12 pairs, 1-2.2 cm long, 0.5-1.0 cm wide, oblong or oblong-obovate, rounded apically, obtuse or asymmetrical basally. Inflorescence pyramidal corymb-like racemes with numerous showy red-orange flowers; pedicels 5-8 cm long, the inferior longer. Sepals 5, imbricated, 5-10 cm long, unequal, lanceolate or obovate, the exterior of larger size. Petals 5, imbricated, conspicuously undulate, obovate, unguiculate, 2-2.5 cm long, 1-1.5 cm wide. Stamens 10, 5-6 cm long; filaments red, pubescent at the base; anthers longitudinally dehiscent. Gynoecium 5-6 cm long, filiform, glabrous, inserted into the bottom

of a hollow receptacle. Legume subligneous, glabrous, oblong, somewhat oblique, 8–12 cm long, 1–2 cm wide.

Exotic species known as "Clavellina"; widely distributed in tropical and subtropical regions of America; cultivated for the beauty of its variety of colour; easily adaptable to any type of soil, being very drought resistant.

Cassia reticulata Willd.

Shrub or small tree 3–5 m high, unarmed, pubescent on young branches. Leaves alternate, pinnately compound; petiole and rachis pubescent; pinnae 9–14 pairs, 5–10 cm long, 2–4 cm wide, oblong, obtuse or rounded apically, oblique or obtuse basally, pubescent below. Raceme with numerous yellow flowers; bracts caducous, conspicuous, membranous, sheathing. Sepals 5, imbricated, 1.3–1.7 cm long, 0.6–0.9 cm wide. Petals 5, imbricated, 1.9–2.1 cm long, 1.1–1.3 cm wide, obovate. Stamens 10, 0.45–1.2 cm long, 3 or 4 sterile, crooked; anthers dehiscent by pores. Gynoecium 1.5–1.7 cm long, curved, pubescent. Fruit linear, oblong, chartaceous or subligneous, shiny, compressed, 10–16 cm long, 1–1.5 cm wide.

Autochthonous species known as "Trantan", 'Brusca'; common in coastal dry forests, frequent on alluvial soils, river shores, gallery forests, marsh and ravine.

WOOD ANATOMY

Caesalpinia coriaria (Jacq.) Willd.

Wood diffused, porous. The basic mass of wood consists of polygonal fibres with thicker walls. Aliform-confluent longitudinal parenchyma in considerable amounts (METCALF and CHALK 1950). The medullary rays are one- or two-cell wide (Fig. 1).

The tracheae are oval and round, in the groups (of 2–5) tangentially flattened. They are 14–25, 4–33 per mm² in number. The tangential diameter is 46.5–67.4–93.0 μ m, the radial diameter 46.5–84.6–120.9 μ m. The members of vessels are 356.5–452.5–655.5 μ m long, with alternate, small elongated bordered pits in the walls. In the tracheae mastic material is rarely found. The perforate plate is simple.

The medullary rays are 1–2-cell wide, generally of homogeneous,

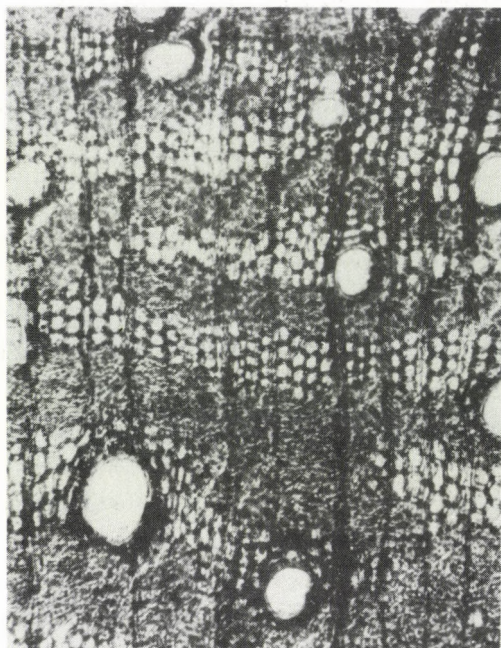


Fig. 1 Caesalpinia coriaria
(Jacq.) Willd. Cross-section
120x. Vessels, medullary rays,
fibres. Aliform-confluent longi-
tudinal parenchyma

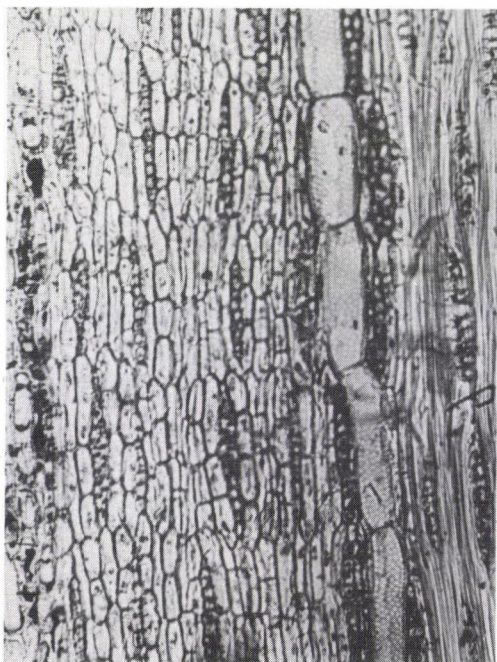


Fig. 2 Caesalpinia coriaria
(Jacq.) Willd. Tangential longi-
tudinal section 120x. One- and
two-cell wide medullary rays,
longitudinal parenchyma, vessel
and fibres. On the wall of the
vessel small, elongated bordered
pits of alternate position

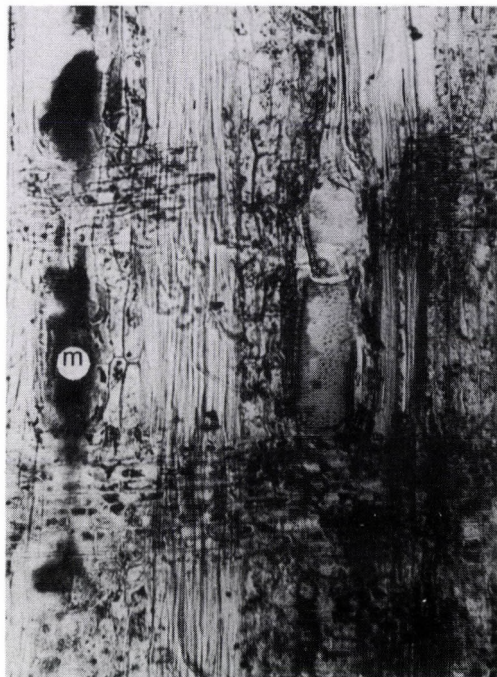


Fig. 3 *Caesalpinia coriaria* (Jacq.) Willd. Radial longitudinal section 120x. Homogeneous medullary rays, vessels, longitudinal parenchyma and fibres. In one of the vessels dark mastic substance. — m = mastic substance

seldom of heterogeneous structure. Thea are $92.0-171.3-920.0 \mu\text{m}$ in height and $11.5-17.3-23.0 \mu\text{m}$ in width. Not often mastic substance is found in the cells of the medullary rays (Figs 2, 3).

The fibres are of irregular position. Their diameter is $9.3-15.8-23.2 \mu\text{m}$, wall thickness $2.3-3.3-4.6 \mu\text{m}$, total length $355.0-643.9-852.0 \mu\text{m}$. The tip of fibre smooth, pointed.

The tangential diameter of the longitudinal parenchyma cells is $4.6-8.8-13.9 \mu\text{m}$, their height is $18.6-34.6-55.8 \mu\text{m}$.

Caesalpinia mollis (H.B. et K.) Spreng.

Dispersedly porous wood. The mass of wood is composed of polygonal fibres with thicker walls and medium lumen. The longitudinal parenchyma is paratrachela, contact-vasicentric, scanty. The medullary rays are 1-2-, not often 3-cell wide. The borders of the growth zones are visible in the wood (Figs 4, 5).

The tracheae are round or oval, in the groups (of 2-3-5) tangentially flattened. They are $24-35.2-54/\text{mm}^2$ in number. Their tangential diameter is $41.8-62.4-88.3 \mu\text{m}$, their radial diameter $37.2-76.8-11.6 \mu\text{m}$. The members

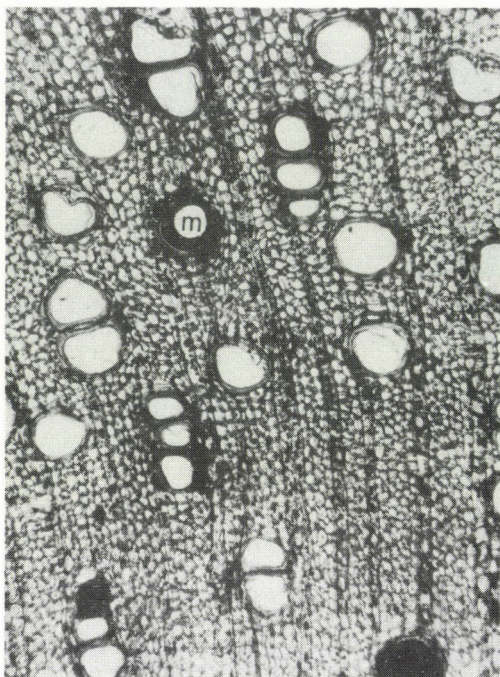


Fig. 4 *Caesalpinia mollis* (H.B. et K.) Spreng. Cross-section 120x. Vessels, groups of vessels, medullary rays and fibres. In the vessels dark mastic material. Contact-vasicentric, scanty longitudinal parenchyma. —
m = mastic material

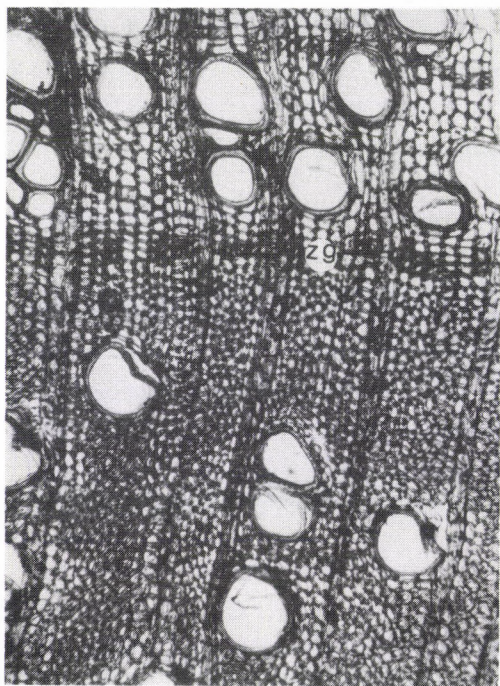


Fig. 5 *Caesalpinia mollis* (H.B. et K.) Spreng. Cross-section 120x. The border of the zone of growth well visible. — zg = zone of growth



Fig. 6 *Caesalpinia mollis* (H.B. et K.) Spreng. Tangential longitudinal section 120x. One- and two-cell wide medullary rays, fibres with thicker walls. Vessel with bordered pits of alternate position. In the medullary ray cells diamond-shaped calcium-oxalate crystal. c = diamond-shaped calcium-oxalate crystal



Fig. 7 *Caesalpinia mollis* (H.B. et K.) Spreng. Radial longitudinal section 120x. Heterogeneous medullary rays, vessel, longitudinal parenchyma and fibres

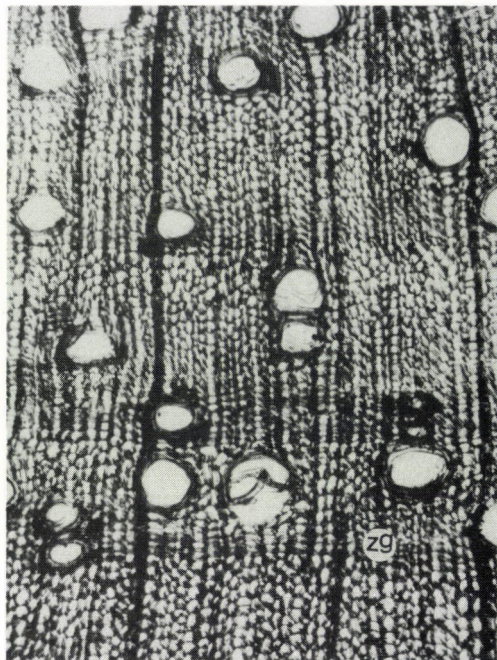


Fig. 8 Caesalpinia pulcherrima
(L.) Sw. Cross-section 120x.
Vessels, groups of vessel, nar-
row medullary rays and fibres.
Contact-vasicentric, scanty
longitudinal parenchyma. — zg =
zone of growth

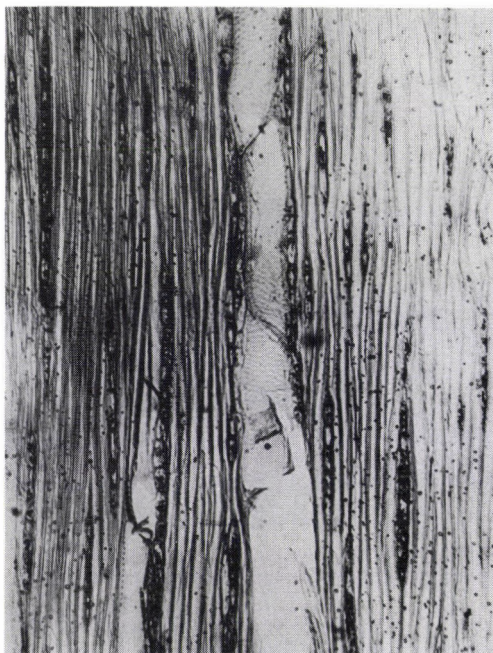


Fig. 9 Caesalpinia pulcherrima
(L.) Sw. Tangential longitudinal
section 120x. One-cell wide
medullary rays, thin-walled
fibres. Vessel with bordered pits
of alternate position



Fig. 10 Caesalpinia pulcherrima
(L.) Sw. Radial longitudinal
section 120. Heterogeneous medul-
lary rays, vessel, longitudinal
parenchyma and fibres

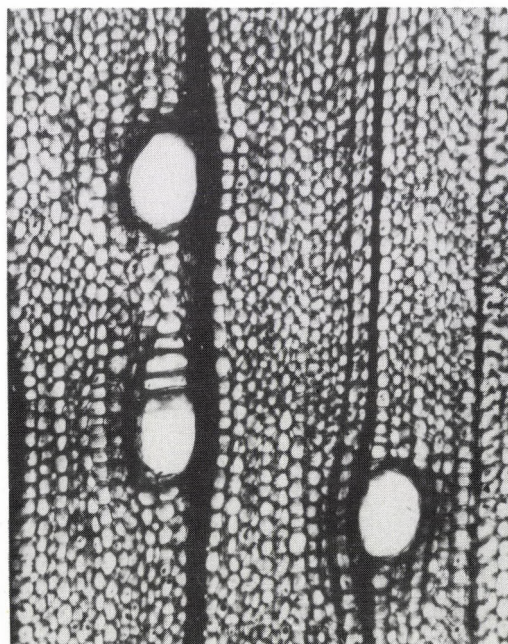


Fig. 11. Cassia reticulata
Willd. Cross-section 120x. Ves-
sels, Group of vessels, narrow
medullary rays and fibres.
Contact-vasicentric scanty
longitudinal parenchyma



Fig. 12 Cassia reticulata
Willd. Tangential longitudinal
section 120x. One-, two- and
three-cell wide medullary rays,
thin-walled fibres and longi-
tudinal parenchyma

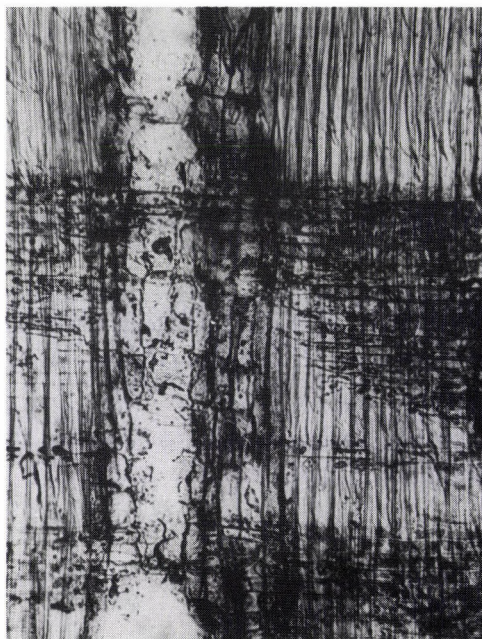


Fig. 13 Cassia reticulata
Willd. Radial longitudinal sec-
tion 120x. Heterogeneous medul-
lary rays, vessel, longitudinal
parenchyma and fibres

of vessel are 289.0–557.1–805.0 μm long. On the walls of the vessels alternately set bordered pits of medium size are found. Mastic substance of dark colour is not infrequent in the tracheae (see the place marked in Fig. 4). The perforate plate is simple.

The medullary rays are 1–2- sometimes 3-cell wide, with a heterogeneous structure. Their height is 126.5–242.0–586.5 μm , their width 17.2–24.6–34.5 μm . Diamond-shaped calcium oxalate crystals are not infrequent in the medullary ray cells (Figs 6, 7).

The fibres are arranged in irregular or radial rows. Their diameter is 9.3–13.6–18.6 μm , their wall-thickness 2.3–3.7–4.6 μm . The total length of fibres is 355.0–668.1–994.0 μm . The tip of fibre is smooth, pointed.

The tangential diameter of the longitudinal parenchyma cells is 4.6–5.6–9.3 μm , their height is 18.6–31.3–41.8 μm . Locular crystal holder longitudinal parenchymae are not infrequent.

Caesalpinia pulcherrima (L.) Sw.

Wood with diffused pores. The mass of wood is produced by polygonal fibre of thinner wall and medium lumen. The medullary rays are narrow. The longitudinal parenchyma is paratracheal, contact-vasicentric, scanty. The borders of the growth zones can be recognized in the wood (Fig. 8).

The tracheae are roundish or oval, in the groups of 2–4 tangentially flattened. They are 23–33.6–45/mm² in number. The tangential diameter is 41.8–57.5–83.7 μm , the radial diameter 46.5–69.4–88.3 μm . The members of vessel are 310.5–574.4–747.5 μm long, with alternately set tiny bordered pits on the walls. In the tracheae mastic substance is seldom found. The perforate plate is simple.

The medullary rays are 1–2-cell wide, of heterogeneous structure. They are 69.0–205.2–379.5 μm high and 5.75–12.3–23.0 μm wide. In the medullary ray cells mastic substance is seldom found (Figs 9, 10).

The fibres are arranged in radial rows. The diameter is 9.3–14.3–18.6 μm , the wall thickness 1.1–2.3–4.6 μm . The total length of fibre is 426–620.5–852.0 μm . The tip of fibre is smooth, short, pointed.

The tangential diameter of the longitudinal parenchyma cells is 4.6–5.0–6.9 μm . Their height is 13.9–37.6–55.8 μm . Locular, crystal holder longitudinal parenchyma rarely occurs.

Table 1
Anatomical features of the species examined

Wood elements	Features	<i>Caesalpinia corinaria</i>	<i>Caesalpinia mollis</i>
Trachea	arrangement	diffused, solitary or in radial groups of 2-5 members	diffused, solitary or in radial groups of 2-3-5 members
	shape	roundish or oval shaped in groups in tangential direction flattened 93.0	roundish or oval shaped in groups in tangential direction flattened
	tangential diameter	46.5-67.4 μm	41.8-76.8-88.3 μm
	radial diameter	46.5-84.6-120.9 μm	37.2-76.8-111.6 μm
	length of vessels	356.6-452.5-655.5 μm	289.0-557.5-805.0 μm
	number per mm ²	14.0-25.4-33.0	24.0-35.2-54.0 μm
	wall thickness	4.7-5.7-9.3 μm	2.3-4.8-9.3 μm
	intervascular pitting	elongated bordered	bordered
	perforate plate	simple	simple
	content	rarely mastic material	mastic material
Medullary rays	width	11.5-17.3-23.0 μm	17.2-24.6-34.5 μm
	number of cells	1-2	1-2, rarely 3
	classification	homogeneous, rarely heterogeneous	heterogeneous
	height	92.0-171.3-920.0 μm	126.5-242.1-586.5 μm
Fibers	width	4.6-6.9-9.3 μm	6.9-9.9-13.9 μm
	content	—	calcium oxalate crystal
	arrangement	irregular	irregular or in radial rows
	shaped	polygonal	polygonal
	full diameter	9.3-15.8-23.2 μm	9.3-13.6-18.6 μm
	wall thickness	2.3-3.3-4.6 μm	2.3-3.7-4.6 μm
	full length	355.0-643.9-852.0 μm	355.0-668.1-994.0 μm
	type of pitting	small, bordered	small, bordered
Longitudinal parenchyma	arrangement	aliform-confluent	contact-vasi-centric scanty
	diameter	4.6-8.8-13.9 μm	4.6-5.6-9.3 μm
	height	18.6-34.6-55.8 μm	18.6-31.3-41.8 μm
	number of cells	4-6-8	2-4-6
	content	diamond-shaped calc. ox. crystal	diamond-shaped calc. ox. crystal
	others	locular crystal holder long. parenchyma	locular crystal holder long. parenchyma

Table 2

Anatomical features of the species examined

Wood elements	Features	<u>Caesalpinia</u> <u>pulcherrima</u>	<u>Cassia</u> <u>reticulata</u>
Trachea	arrangement	diffused, solitary and radial groups of 2-4 rarely 5 members	diffused, solitary rarely in radial groups of 2-3 members
	shape	roundish or oval	roundish or oval
	tangential diameter	41.8-57.5-83.7 μm	65.1-85.4-102.3 μm
	radial diameter	46.5-69.4-88.3 μm	69.7-110.1-148.8 μm
	length of vessels	310.5-574.4-747.5 μm	448.5-643.1-908.5 μm
	number per mm ²	23.0-33.6-45.0	5.0-8.9-15.0
	wall thickness	2.3-3.8-6.9 μm	2.3-3.4-4.6 μm
	intervascular pitting	bordered	elongated bordered
	perforate plate content	simple rarely mastic material	simple —
Medullary rays	width	5.75-12.3-23.0 μm	11.5-23.2-34.5 μm
	number of cells	1-2	1-3
	classification	heterogeneous	heterogeneous, rarely homogeneous
	height	69.0-205.2-379.5 μm	69.0-282.5-575.0 μm
	width content	5.7-12.3-23.0 μm rarely mastic material	11.5-23.2-34.5 μm mastic material
Fibres	arrangement	in radial rows	irregular or in radial rows
	shape	polygonal	polygonal
	full diameter	9.3-14.3-18.6 μm	13.9-18.4-27.9 μm
	wall thickness	1.1-2.3-4.6 μm	1.1-2.8-4.6 μm
	full length	426.0-620.5-852.0 μm	355.0-631.1-852.0 μm
	type of pitting	small bordered	with split
Longitudinal parenchyma	arrangement	contact-vasicentric, scanty	contact-vasicentric, scanty
	diameter	4.6-5.1-6.9 μm	4.6-8.3-11.6 μm
	height	13.9-37.6-55.8 μm	18.6-36.2-93.0 μm
	number of cells	2-4	2-6
	content	diamon-shaped calc. ox. crystal	—
	others	locular crystal holder long. parenchyma	—

Cassia reticulata Willd.

Wood with diffused pores. The mass of wood is given by the polygonal fibres of thinner wall and medium lumen. The medullary rays are narrow. The longitudinal parenchyma is paratracheal, contact-vasicentric, scanty (Fig. 11).

The tracheae are roundish or oval; in the groups (of 2-3) tangentially flattened. They are $5-8.9-15/\text{mm}^2$ in number. The tangential diameter is $65.1-85.4-102.3\ \mu\text{m}$, the radial diameter $69.7-110.0-148.8\ \mu\text{m}$. The members of vessel are $448.5-643.1-908.5\ \mu\text{m}$ long, with alternately set, elongated, bordered pits of medium size on the walls.

The medullary rays are 1-2- or 3-cell wide, of heterogeneous, seldom homogeneous structure. They are $690-282.3-575.0\ \mu\text{m}$ high and $11.5-23.2-34.5\ \mu\text{m}$ wide. In the medullary ray cells mastic substance is not infrequently found (Figs 12, 13).

The fibres are arranged in irregular or radial rows. The diameter is $13.9-18.4-27.9\ \mu\text{m}$, the thickness of wall $1.1-2.8-4.6\ \mu\text{m}$. The total length of fibre is $355.0-631.1-852.0\ \mu\text{m}$. The tip of fibre is smooth, short, pointed.

The tangential diameter of the longitudinal parenchyma cells is $4.6-8.3-11.6\ \mu\text{m}$, their height is $18.6-36.2-93.0\ \mu\text{m}$.

The detailed anatomical features and measurements of wood in the four tree species are contained in Table 1 and 2.

REFERENCES

- Metcalfe, C.R., Chalk, L. (1950): Anatomy of the Dicotyledons. Vol. I. Clarendon Press, Oxford, 493-495.
- Sárkány, S., Szalai, I. (1964): Novényszervezettani gyakorlatok (Plant Anatomical Practicum). (In Hungarian). Tankönyvkiadó, Budapest, 559.

COMPARATIVE STUDY OF THE IRIDOID PRODUCTION OF HUNGARIAN AND GEORGIAN
GALIAM VERUM L. POPULATIONS

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Galium verum L. populations originated from Central Europe (Hungary) and from the Caucasus (Georgia) were introduced to the Botanical Garden of the Institute of Ecology and Botany of the Hungarian Academy of Sciences, to Vácrátót. Both populations were analyzed for phytomass, iridoid percentage and iridoid production. They do not differ considerably in iridoid composition; asperuloside is the main component in both. The minor components do not show differences evaluable from chemotaxonomic point of view. As regards the phytomass and the iridoid content, Hungarian population turned to be more favourable than the Georgian one, giving higher yield in both respect. On this basis they may consider as a higher production Central European and a lower production Caucasian ecotype.

INTRODUCTION

On the chemistry, determination methods, biological activity and chemotaxonomic evaluation of iridoid monoterpene glycosides numerous monographs have been published (STICHER 1975, JENSEN et al. 1975, STICHER 1977). Little information can be found, however, on the variability of these compounds wide-spread in the flora, and publications on their production are almost non-existent (HEGNAUER 1973).

Iridoid examinations covering species of the family Rubiaceae, first of all those native in Hungary, began in 1978.

Of the Asperula and Galium species native in Hungary we chose G. verum L. as a model plant for studying the variability of the iridoid production. The plant was made suitable for this purpose by its wide distribution and its relatively long vegetation period. As another favourable circumstance, the iridoid content of the plant has been studied since the 1920s,

and so, in comparison to other species, the available information concerning the plant is rather reliable.

According to BÜJTHER-HORVÁTH et al. (1982), MÁTHÉ et al. (1981) HÉRISSEY, KOHLMÜNZER, BORISHOV, SWIATEK obtained asperuloside from G. verum as main iridoid component, which gave positive reaction with the TRIM-HILL reagent (TRIM 1952), beside many minor components such as monotropeine, scandoside, deacetyl-asperulosidic acid, asperulosidic acid, geniposidic acid, as well as a structurally less known V_1 compound (BÜJTHER-HORVÁTH et al. 1982). It is also possible that even in a freshly processed plant sample (e.g. while chromatographed) artificial products arise increasing the quantity of the minor components (BÜJTHER-HORVÁTH et al. 1982). However, the amount of minor components compared to the asperuloside, the main component is negligible.

Our earlier examinations were concentrated on the evaluation of the Hungarian G. verum populations. In successive years we evaluated from about 70 different growing sites the amount of the phytomass per shoot, per organ within the shoot, its iridoid i.e. asperuloside content, and on the basis of the information thus obtained its asperuloside production. We also obtained data on the accumulation of 10 major soil nutrients and established correlations between their quantities and the parameters of production (MÁTHÉ jr. et al. 1981, 1984). We wished to check the data concerning the Hungarian populations by comparing them with a population from a different geographic region. For this purpose we established cooperation with the Institute of Pharmacochemistry of the Georgian Academy of Sciences and started researches for the comparison of the Hungarian and Georgian G. verum populations, some results of them are reported in this paper.

MATERIAL AND METHOD

In 1980 flowering Galium verum L. shoots were collected from various parts of Hungary and Georgia (in the latter case from different heights above sea level). After drying at 80 °C the leaves, the stems and the inflorescences were weighed separately, and so was the phytomass of the vegetative shoots according to our earlier elaborated method (MÁTHÉ jr. et al. 1981).

In 1981 1 m² plots were sown with Hungarian and Georgian seed (1 and 2 g/m², respectively) on the area of the Institute of Ecology and Botany of the Hungarian Academy of Sciences. Throughout the whole vegetation period, from the beginning of May to the end of August, phytomass was collected every second week, weighed organ by organ, and determined for iridoid content through the Trim-Hill reaction.

On the quantitative proportions of asperuloside and its associate components information was obtained from the analysis of alcoholic extracts of freshly collected samples: 5 g of freshly collected material was rubbed with 70% ethanol in the presence of calcium carbonate, then the extracted juice was completed (by flushing) to a standard volume (25 ml). From the stock solution 10 μ l was applied to aluminium oxide layer, and chromatographed with dichloromethane-methanol-water (32+11+1.6) (A) and ethyl acetate-i-propanol-water (6+3+1) (B) mixtures. For developing the Trim-Hill reagent (14) was used (with 100 ml acetic acid + 5 ml hydrochloric acid added to 10 ml 0.2 % aqueous solution of copper sulphate). The chromatographic procedure performed in the presence of asperuloside obtained from the Institute of Organic Chemistry of the Semmelweis Medical University was accomplished by the evaluation of blue spots evoked by heating following the application of the reagent (TRIM 1952).

The Trim-Hill reaction was used to evaluate the iridoid content of the drugs as well: 0.5 g dried drug or freshly collected drug equivalent to it was measured out, boiled for 15 minutes with distilled water in the presence of calcium carbonate, then the aqueous extract was poured off, and filtered through aluminium oxide layer to purify. The solution was completed to 100 ml, then with 11 ml Trim-Hill reagent added to each ml heated for 5 minutes, and determined at 604 nm wavelength by photometry for iridoid content expressed in asperuloside. Between the quantitative values of fresh and dried samples no significant difference was found.

The quantity and composition of antraglycosides occurring in relatively large amounts in the roots of G. verum populations (BORISHOV et al. 1971, 1976) were compared to the composition of root extract from Rubia tinctorum with the method of FORMANEK (1970) used.

DISCUSSION

The iridoid composition of freshly collected Hungarian and Georgian G. verum samples has been evaluated by means of chromatograms. The chromatograms obtained in two different systems seem to confirm the earlier statement that asperuloside is the main iridoid component of G. verum. Both in the Georgian and Hungarian populations varying quantities of minor components were also found. On this basis, however, no considerable differences between the two populations could be pointed out.

Table 1 contains the production data of shoots of G. verum plants collected from different habitats of Hungary and Georgia. In the case of the Georgian samples the data are grouped according to height intervals.

As seen from the table the samples of Hungarian origin as a whole give more favourable production averages than those from Georgia. Some fractions of sample suggest that there are exceptions to the rule, e.g. as for the iridoid percentage of the leaf the averages of Georgian samples from the heights of 400 and 500–1000 m above sea level are more favourable.

The fact that in the Georgian samples the percentage values of

Table 1

Production data of Galium verum shoots of Hungarian and Georgian origin (July–August, 1981)

Height	Vegetative Shoots			F l o w e r i n g									Shoots Total	
				Leaf			Stem			Inflorescence				
	1.	2.	3.	1.	2.	3.	1	2.	3.	1.	2.	3.	1.	3.
Hungarian														
–500 \bar{x}	0.33	2.96	8.9	0.34	0.76	6.3	1.23	0.62	5.9	0.49	4.35	20.1	1.97	33.4
n=35 $\pm s$	0.03	0.38	1.1	0.03	0.16	0.8	0.11	0.06	1.0	0.06	0.22	2.2	0.16	2.9
Georgian														
–500 \bar{x}	0.39	2.47	9.3	0.26	2.71	7.1	0.47	0.34	1.4	0.20	4.19	8.4	0.92	16.9
n=3 $\pm s$	0.07	0.79	3.5	0.04	0.43	2.1	0.06	0.14	0.5	0.02	0.51	2.2	0.11	3.4
500–1000 \bar{x}	0.17	1.06	1.84	0.21	1.82	4.5	0.65	0.20	1.2	0.52	4.19	20.6	1.38	26.2
n=7 $\pm s$	0.01	0.12	0.25	0.03	0.38	1.3	0.12	0.06	0.4	0.14	0.36	6.1	0.18	7.1
1000–1500 \bar{x}	0.18	1.51	2.7	0.22	0.59	1.3	0.99	0.0	0.0	0.33	3.34	10.5	1.53	11.8
n=6 $\pm s$	0.02	0.39	0.8	0.02	0.18	0.40	0.22			0.06	0.19	1.4	0.28	1.5
1500– \bar{x}	0.17	1.06	1.8	0.18	1.01	1.8	1.06	0.15	1.9	0.35	3.24	11.4	1.59	1.15
n=9 $\pm s$	0.01	0.12	0.2	0.02	0.24	0.5	0.14	0.07	0.8	0.06	0.11	2.3		2.8

1: Phytomass (g); 2: Iridoid (dry wt. %); 3. Iridoid production (mg)

iridoid change in inverse proportion to the height appears only as a tendency. The scatter of phytomass data does not show unequivocal changes by the height. It was only in the case of the stem that the values were found to increase with the height.

According to the data of the table G. verum populations in the Caucasus not only occur up to about 2000 m, but do not even show considerable changes in phytomass- and iridoid production.

The G. verum samples obtained from natural habitats in Hungary and Georgia are characterized in Fig. 1. by average values too. As regards both the phytomass and the iridoid content (iridoid percentage) and production the Hungarian population appears to be more favourable. This statement is supported by the significance analysis of the differences between the parameters examined. For most parameters the differences proved significant at 0.1 and 5% level, respectively.

Changes during the vegetation period in populations of Hungarian and Georgian origin raised from seed for the trial area of the Institute of Ecology and Botany of the Hungarian Academy of Sciences in 1981 were generally followed in 1982 by samples taken every second week. In Fig. 2 the data of phytomass per shoot are seen. As shown by the figure the Hungarian and Georgian samples give highly similar curves.

The minima appearing in the middle of the vegetation period were due to the fact that the decrease in the number of developed shoots collected continuously from the 1 m² area was more rapid than the development of shoots, so the latter could not keep abreast with the intensity of sampling. In the second half of July, mainly in consequence of the abundant rainfalls (Table 2), the development of the populations became more intensive again, as indicated by the appearance of the second maximum, producing — so to say — a second vegetation period. The curves clearly show the excellent regenerative capacity of the populations after cutting. The different origin of populations do not show difference in this respect either.

Having compared the shoot production of the two populations organ by organ on each occasion of sampling we obtained the average values of difference seen in Table 3 for the total period of vegetation. Statistically demonstrable differences between the two populations were only found in the case of inflorescence and total shoot production.

In this table the data of the Hungarian and Georgian samples are given with the results of a regression analysis also taken into considera-

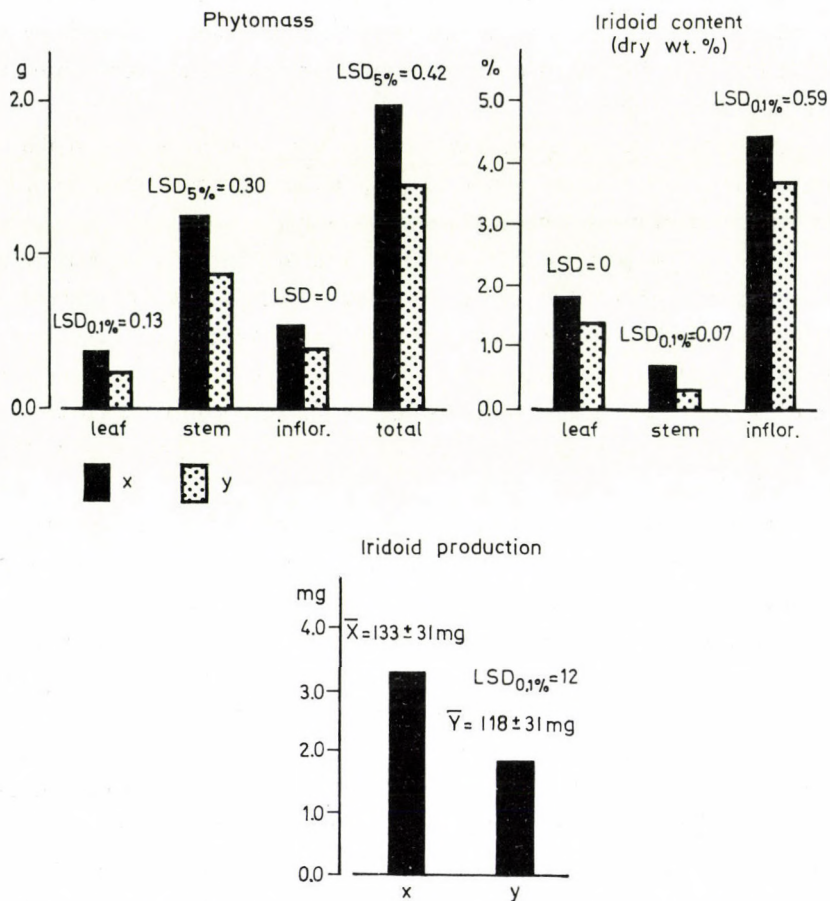


Fig. 1 Production parameters of *Galium verum* L. shoots originated from natural habitats. X = Hungarian populations (In = 360); Y = Georgian populations (In = 261)

tion. In each case a positive correlation was found. The correlation coefficients show close to medium close correlations for the organs and total phytomass of the two stands. These data again indicate that — as expected on the basis of the diagrams in Fig. 2 — the changes of production in the two stands are parallel and show the same trend.

Table 4 contains the iridoid contents per organ of the Hungarian and Georgian stands grown under conditions of Hungary. The values expressed in asperuloside percentage appear to be more favourable with the Hungarian population. (The scatters of the values given in the table were calculated on the basis of samples taken during the whole vegetation period; for aver-

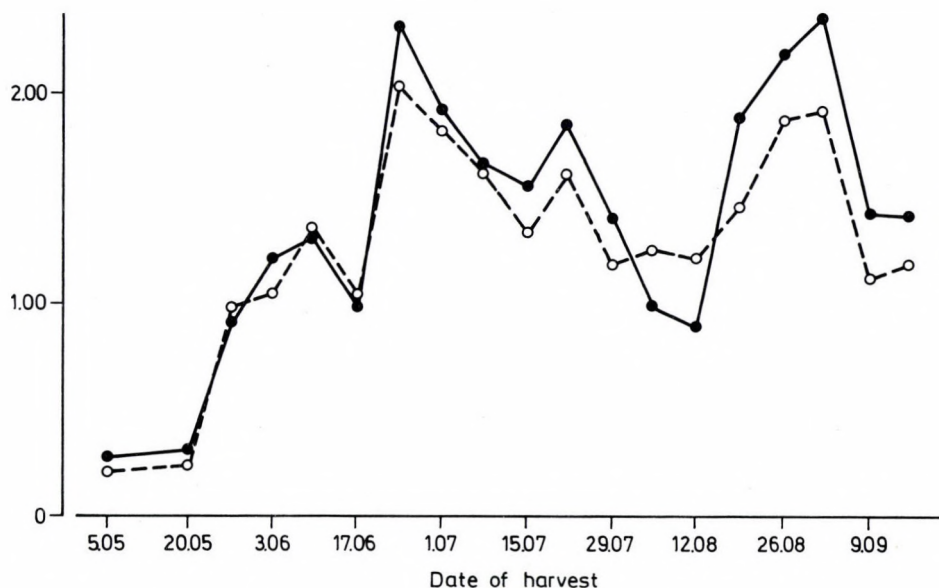


Fig. 2. Shoot biomass harvested biweekly in the vegetation period of 1982
 — Hungarian, --- Georgian population

aging and calculating the scatters the differences were determined by pairs.)

Figure 3 shows the iridoid production values calculated on the basis of the phytomass- and iridoid percentage values. Both populations gave maximum values more or less in the same period: July. We also examined the two populations for correlations between their data; similarly to the phytomass, the Georgian samples were evaluated as a function of the Hungarian ones. The medium close correlation obtained in this case too indicates that the two stands showed similar changes. A comparison of the data of each sampling reveals a difference between the two populations significant at 0.1% level.

The microplots established on the trial grounds of Vácrátót rendered comparisons per unit area also possible. Of the production data shown in Table 5 the phytomass average of the Georgian samples was higher per unit area, although with the scatter of the data considered the difference is not significant. (This deviation from the values of phytomass per shoot may be explained by the difference in stand density.) All the other values were more favourable in the Hungarian samples, out of them

Table 2

Meteorological data in the vegetation period (1982; BP KLFI)

Time (intervals)	01.04— 05.05	06.05— 20.05	21.05— 03.06	04.06— 17.06	18.06— 01.07	02.07— 15.07	16.07— 29.07	30.07— 12.08	13.08— 26.08	27.08— 09.09
Mean temp. (C ⁰)	12.2	16.9	19.6	19.1	19.6	20.5	22.9	21.9	20.8	20.1
Sunshine (h)	48	100	105	98	106	109	97	123	135	88
Precip. (mm)	1	13	46	22	7	19	76	23	12	6

Table 3

Correlation between the phytomass (g) of *G. verum* shoots of Hungarian (X) and Georgian (Y) origin (Vácrátót; 1982)

X	Y	n	regr. coeff. (b)	corr. coeff. (r)	$\frac{\sum(X-Y)}{n}$	LSD
Leaf — Leaf		16	0.507	0.84	0.04	
Stem — Stem		16	0.662	0.91	0.03	
Inflor.—Inflor.		16	0.673	0.85	0.06	0.05 ⁺
Total—Total shoots		19	0.787	0.94	0.13	0.10 ⁺⁺

⁺P = 10%; ⁺⁺P = 5%

Table 4

Iridoid content (dry mass. %) of Hungarian and Georgian Galium verum stands in the vegetation period of 1982 (Vácrátót)

	Hungarian		Georgian		LSD
	\bar{X}	$\pm S$	\bar{X}	$\pm S$	
Leaf	1.17	0.36	0.78	0.25	0.32 P=5%
Stem	0.85	0.27	0.37	0.20	0.39 P=0.1%
Inflor.	2.30	0.81	1.68	0.50	0.50 P=5%
Shoot ⁺	1.47	0.54	0.86	0.30	0.57 P=0.1%

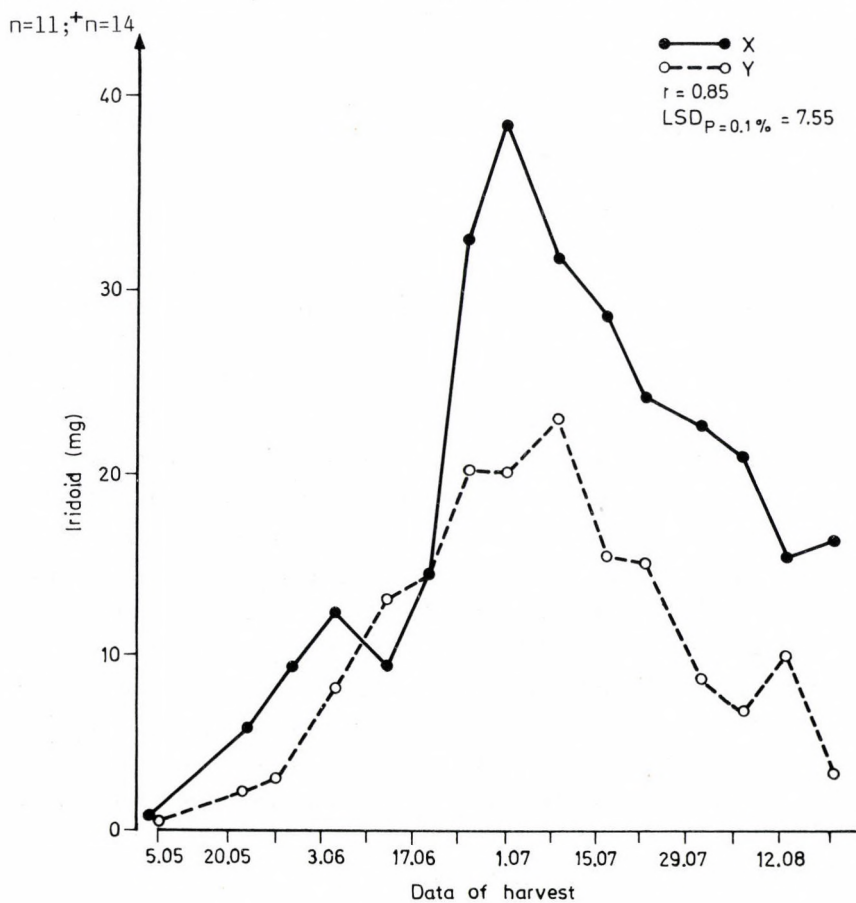


Fig. 3 Variation in the iridoid production of shoots of Galium verum L. populations of Hungarian (X) and Georgian (Y) origin (Vácrátót, 1982, n=3)

Table 5
Production data from 1 m² parcels (Vácrátót; 7. 07. 1983)

	POPULATION ($\bar{X} \pm \frac{s}{\sqrt{n}}$)	
	Hungarian (n=20)	Georgian (n=5)
Above-ground		
Phytomass (g)	391 [±] 41	462 [±] 70
Iridoid (%)	1.03 [±] 0.09 ⁺	0.63 [±] 0.06 ⁺
Iridoid (g)	3.87 [±] 0.46	2.86 [±] 0.44
Roots		
Phytomass (g)	779	686
Iridoid (%)	0.93	—
Anthraquinones (%)	1.18	0.81
Anthraquinones (g)	9.18	5.56

⁺LSD_{5%} = 0.36

only the averages of the iridoid percentage showed statistically proved differences.

We used the determination method of FORMANEK (1970) to receive information on the amount of anthraquinon derivatives accumulating in the root of G. verum. Table 5 shows — among others — that the Hungarian samples proved somewhat more favourable than the Georgian ones in respect of this parameter as well. Nevertheless, we wish to emphasize that our composition data — while not differing from those of the Rubia tinctorum extract — can be regarded as of informative character only, since we have not carried out detailed analyses aimed at isolating the anthraquinones, and as the root in question was difficult to clean, even the quantitative values are only approximative. In spite of all this the anthraquinon production of G. verum seems to be similar to that of R. tinctorum to such an extent that the former can practically replace the latter in regions where the R. tinctorum is not at home.

CONCLUSIONS

G. verum populations of distant geographic regions partly collected from original habitats for the purpose of analysis, partly introduced in the same area in Hungary were compared for phytomass, iridoid percentage and iridoid production. The examinations have led to the following conclusions.

— There is no considerable difference in iridoid composition between the two populations, asperuloside is the main component in both of them, and the minor components do not show chemotaxonically evaluable differences.

— The production data, on the other hand, were found to be different for the two populations. The Hungarian samples were more favourable than the Georgian ones as regards both the phytomass and the iridoid content. This difference appeared both with plants collected from the original habitats and with stands exposed to the same ecological effects under the same conditions, though occasionally only as a tendency.

— Populations originating from the two regions underwent similar changes in response to the same environmental influence. (E.g. during the vegetation period similar production curves were obtained.)

To sum it all up we can state that samples collected from populations more than thousand km far from one another in the area of G. verum as well as stands of different origin raised from seed under the same conditions showed marked differences in production. On this basis it might be justified to speak of a higher production Central European- and a lower production Caucasian G. verum ecotype. Latter may perhaps be described as an alpine type, provided that further investigations point out a closer connection between altitude and production.

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REFERENCES

- Borishov, M.I. (1976): Antrakhinovi glikozidi Asperula besseriana Klok. i Galium ruthenicum Willd. Rast. Res. **12**: 362–368.
- Borishov, M.I., Zsralev, N.S., Iskova, T.I. (1976): Kolichestvennoe soderezhaniye flavonoidon rasteniah rodov Asperula L. i Galium L. Rast. Res. **11**: 351–258.
- Böjthe-Horváth, F., Hetényi, Á., Kocsis, L., Szabó, M., Varga-Balázs, I. Máthé, jr., P. Tétényi (1982): Iridoid glycosides from Galium verum. Phytochemistry **21**: 2917–2919.
- Formanek, Gy. (1970): A festőbuzér (Rubia tinctorum L.) antrakinson származékainak értékmeghatározási módszereiről (Methods of determining the value of anthraquinon derivatives from Rubia tinctorum L.). Orvosi Szemle **16**: 206–211.
- Hegnauer, R. (1973): Chemotaxonomie der Pflanzen **6**: 132. Birkhauser Verlag, Basel–Stuttgart.
- Jensen, S.P., Nielsen, B.J., Dahlgren, R. (1975): Iridoid compounds, their occurrence and systematic importance in the Angiosperms. Bot. Notiser **128**: 148–180.
- Máthé, I. jr., Vadász, Á., Máthé, I. (1981): Galium verum L. populációk asperulozid produkciójának összehasonlító vizsgálata a budapesti agglomeráció területén (Comparative study of the asperuloside production of Galium verum L. populations on the agglomeration area of Budapest). Bot. Közlem. **68**: 77–84.
- Máthé, I. jr., Vadász, Á., Máthé, I., Tétényi, P., Szabó, L. (1982): Magyarországi Galium fajok iridoid tartalmának vizsgálata Trim-Hill reakció alapján (Analysis of iridoid content in Hungarian Galium species on the basis of the Trim-Hill reaction). Herba Hungarica **21**: 185–196.
- Máthé, I. jr., Vadász, Á., Máthé, I., Máthé, Á., Tétényi, P. (1984): Variation in the asperulosid production of Galium verum L. during the vegetation period. Acta Horticulturae **144**: 49–56.
- Sticher, O., Junod-Busch. (1975): Die Iridoidglucoside und ihre Isolierung. Pharm. Acta. Helv. **50**: 127–144.
- Sticher, O. (1977): Die Gehaltsbestimmung von Iridoiddrogen. Pharm. Acta Helv. **52**: 12. 20–32.
- Sticher, O. (1977): New natural products and plant drugs with pharmacological, biological or therapeutical activity. 137–176. (ed. Wagner, H., Wolff, P.) Springer Verlag, Berlin–Heidelberg–New York.
- Trim, A.R. (1952): Preparation and properties of aucubin asperuloside and some related glycosides. Biochem. J. **50**: 310.

EFFECT OF MNNG, A CHEMICAL CARCINOGEN ON THE DEVELOPMENT OF SUNFLOWER
(HELIANTHUS ANNUUS L.) AND THE TISSUE STRUCTURE OF ITS STALK

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The effect of N-methyl-N-nitroso-N'-nitroguanidine (MNNG) — a well known chemical carcinogen which does not require metabolic transformation for its activity — was studied by in vivo use of sunflower, a plant with high biological responsiveness.

It was found that MNNG when added once to the culture fluid of the plant at rates of 1, 5 and 10 µg/ml, respectively, caused the following changes:

- 1) the lowest dose was ineffective compared to the control;
- 2) with the concentrations 5 and 10 µg/ml the initial normal development of the plant stopped on the 11th day following the treatment — relatively late —, further leaves and lateral roots did not form, the main root showed signs of necrosis;
- 3) the number of cell-rows in the collenchyma and sclerenchyma and the thickness of cell-wall in these tissues considerably decreased compared to the control with the increase of dose, which may suggest a toxic effect;
- 4) visible tumour was not, though, observed, but the histological examination revealed a conspicuous cell proliferation caused by the largest dose in the cortical parenchyma, without atypia characteristic of malignant tumours in mammals.

In the experiment MNNG proved toxic to the whole of the plant, and with a type of cell resulted in proliferation, in tumour-like lesion. MNNG is thus able to induce cell proliferation not only in the case of mammalian cells but also in plants.

INTRODUCTION

The chemical carcinogens are such biologically active substances as inducing tumours in humans and animals. The tissue structure of the malignant tumour is characterized by cell atypia both in mammals and lower animals. In plants tumours of the same structure showing atypia and producing metastasis are not known, but characteristic cell proliferations,

tumour-like conditions do occur. They may develop spontaneously, or can be induced with various physical, chemical and biological (bacterium, virus, insect) agents (BRAUN-STONIER 1958, HERDI 1986, MARÓTI 1976).

Hyperplasia and hypertrophy were observed by PIZZOLATO and REGEHR (1981) and SOROKIN et al. (1962) in peas and tomatoes treated with 2,4-D, 2,4-DB and IAA. Proliferation and enlargement of cell in response to treatment with 2,4-D occurred in other cultivated plants (bean, sunflower, maize) and weeds too (ALLARD et al. 1973, FELBER 1948, KIERMAYER 1964, MURRAY and WHITING 1947, TUKEY et al. 1945).

The herbicide Dicamba caused a tumour-like growth on the leaf of sunflower, in which tracheide, an element of the vascular bundles was found in great masses (HERDI 1986). Similar histological picture can be observed in other tumour-like lesions of the sunflower (BRAUN-STONIER 1958). Tumour-like growths induced by hormone-type herbicides were observed in brassicaceous plants as well (ARLT and FEYERABEND 1982). In onions MCPA, 2,4-D, 2,4,5-T and 2,4,5-trichlorophenol caused developmental deformities (FISKESJÖ et al. 1981).

The experiment was aimed at finding out what the effect of MNNG (N-methyl-N-nitroso-N'-nitroguanidine) — a well-known direct action chemical carcinogen — on the tissues of plants, more closely of sunflower, was and whether it would be able to induce cell proliferation, i.e. tumour-like lesion.

MATERIAL AND METHOD

The test plant was sunflower (*Helianthus annuus* L.) raised in soil under glasshouse conditions. At a development stage of 2-3 foliar leaves the plants were removed from the soil, then — with the roots first washed — placed in Knop's macroelement solution (MARÓTI 1976). The culture fluid was of the following composition: $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ — 500 mg/1000 ml water, KNO_3 — 125 mg/1000 ml water, $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ — 125 mg/1000 ml water, KH_2PO_4 — 125 mg/1000 ml water. The pH of the culture fluid was 7, because according to some authors' experiences (McCALLA et al. 1968, SCHAPER 1970) the decomposition of MNNG slows down at that value of pH. In the experiment MNNG (N-methyl-N-nitroso-N'-nitroguanidine, FLUKA, Switzerland) readily solved in water was used.

With the exception of the control group the plants were treated once with 1, 5 and 10 $\mu\text{g}/\text{ml}$ concentrations of MNNG, respectively (FISKESJÖ 1981) added to the culture fluid on the 10th day after they had been placed in the culture fluid. For each treatment five plants were used. The glass vessels used in the experiment were stained dark owing to the photosensitivity of MNNG. In the course of the experiment the effect of MNNG on the over-all development of the plants was followed.

For examination by light microscope samples were taken from the middle of the first internode of the stalk. The samples were fixed in BOUIN's fixative, then imbedded in paraffine. The microtome sections were stained with gentian violet.

In order to make a proper evaluation of the experiment we studied the tissue structure of the sunflowerstalk, and measured the wall thickness in the sclerenchyma cells of the vascular bundles. The measuring data were evaluated by double t-test. Further, we followed the changes in the number of hypodermic cell-rows underlying the epidermis, as well as in the number of cell-rows of the sclerenchyma, phloem and cambium inside the vascular bundles.

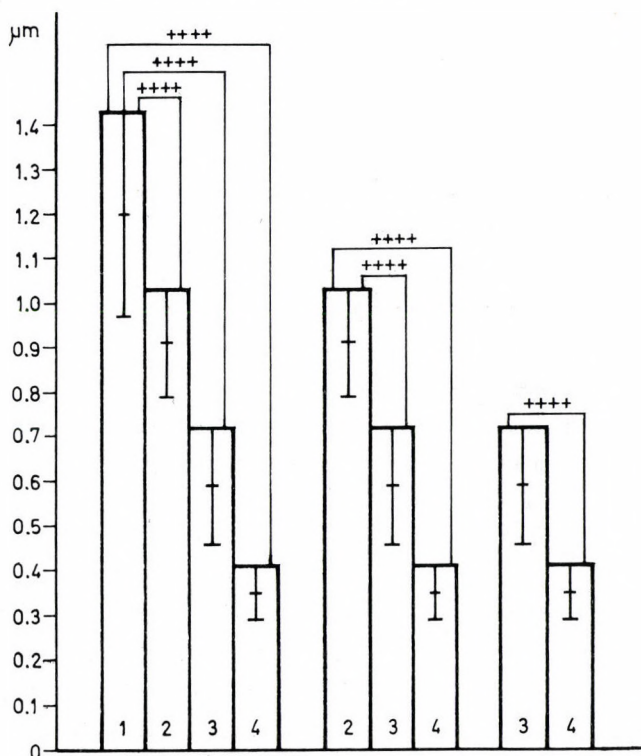


Fig. 1. Changes in the wall thickness of sclerenchyma cells in the vascular bundles of stalk in response to MNNG. 1 = control, 2 = $\mu\text{g/ml}$, 3 = $5 \mu\text{g/ml}$, 4 ($10 \mu\text{g/ml}$, ++++ = $p < 0.1\%$. In all treatments compared to the control, in treatments 3 and 4 compared to treatment 2, in treatment 4 compared to treatment 3: $p < 0.1\%$

RESULTS

Figure 1 shows the wall thickness of schlerenchyma cells in the vascular bundles, and Table 1 contains the number of cell-rows in the elements of the vascular bundles.

1) Macroscopic effects

The control plants were at a development stage of 4 foliar leaves at the time of the treatment. Eleven days later 6 developed and 6 less developed leaves were found on the plants. The leaves showed then a minor degree of chlorosis. The root system was well developed, new lateral roots could be seen to form. On the 22nd day the plants stopped developing, the leaves showed symptoms of chlorosis and necrosis, as the consequences of iron- and microelement deficiency. The root system continued developing.

In the case of 1 $\mu\text{g/ml}$ concentration the plants developed normally during the experiment. Plants at the development stage of 2-3 foliar leaves reached the 5-6-leaf stage by the time of the MNNG treatment. On the 11th day following the treatment 6-7 fully developed and 2-3 less developed leaves were on the plants. Then the plants stopped developing, and the lowest 1-2 leaves dried. During the experiment new lateral roots were formed.

With the 5 $\mu\text{g/ml}$ concentration the plants were of 4-leaf stage at the time of the treatment. The plants were highly responsive to this concentration of MNNG. As early as on the 2nd day after the treatment the cotyledons and the first and second foliar leaves showed symptoms of wilting. On the 11th day the plants were at a 6-leaf stage of development, and each of them had 2 less developed leaves. The first two leaves dried, the next two leaves were found to wilt. The plants stopped developing. During the experiment new lateral roots did not form. The root system displayed brownish spots.

In the case of the 10 $\mu\text{g/ml}$ concentration the plants were at a 4-leaf stage of development at the time of the treatment. The effect was greater than in the former cases. On the 2nd day following the treatment the cotyledons and the first four foliar leaves showed signs of wilting. On the 11th day the first two leaves dried, the plants stopped developing. The root system became totally brown, no further lateral roots developed.

Tumour-like lesions visible to the naked eye were not found either on the control or on the treated plants.

2) Microscopic effects

The stalk of the control plant (Fig. 2) is covered by epidermis

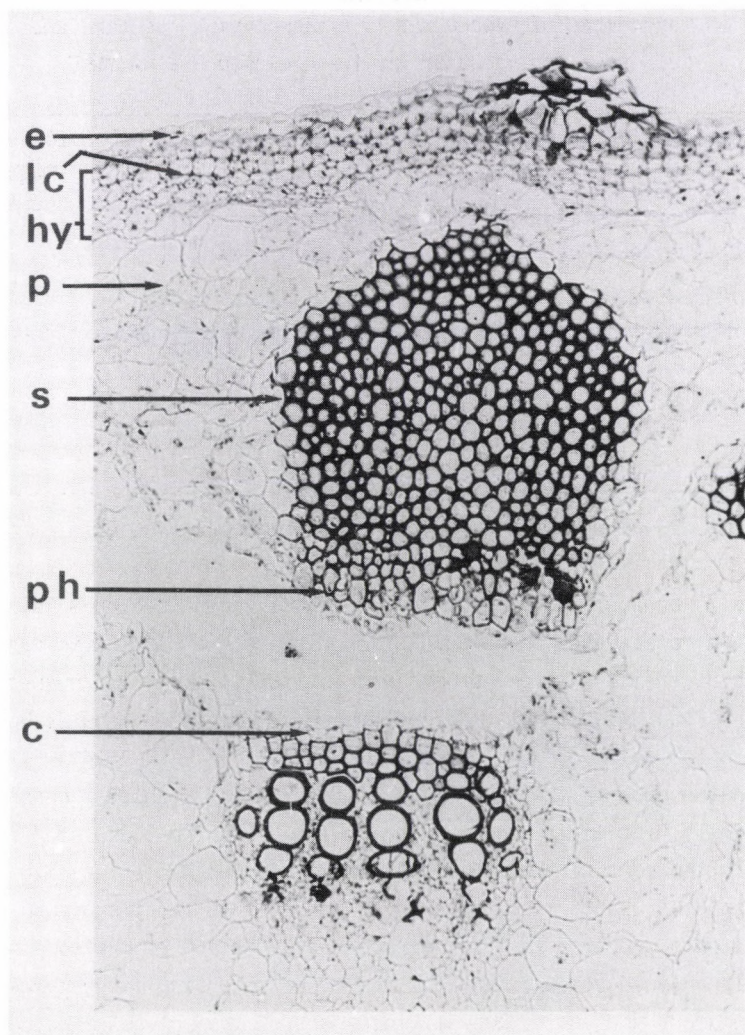


Fig. 2. Part of cross-section from the control (untreated) sunflower stalk with the vascular bundle (e = epidermis, lc = lamellar collenchyma, hy = hypodermis, s = sclerenchyma, p = parenchyma of cortex, ph = phloem, c = cambium) 126x

with multicellular uniseriate- and glandular hair on it. The epidermis cells are closely set, their outer tangential walls are thickened. Under the epidermis a several-row hypodermis is found (Table 1). The lamellar collenchyma cells have thick tangential- and thin radial walls. The width of the hypodermis is not uniform; near the larger vascular bundles the

Table 1

Changes in the number of hypodermis-, sclerenchyma-, phloem- and cambium cell-rows and vascular bundles in response to MNNG

Treat- ment	Hypodermis		Sclerenchyma		Phloem	Cambium	Small	Large
	c e l l - r o w s (n)						vascular	
							bundles (n)	
	in	small	large					
	vascular							
	bundles							
1	1-3	3-5	13-18	3-5	2-3	11	19	
2	3	4-5	6-14	5-6	2-3	5	22	
3	2-4	4-6	5-11	5-9	3-5	5	21	
4	2-4	4-5	4-7	10-12	3-5	5	23	

1 = control - 2 = 1 μ g/ml MNNG - 3 = 5 μ g/ml MNNG - 4 = 10 μ g/ml MNNG

hypodermis is broader, while in the vicinity of those developed later it is narrower. The collateral open vascular bundles show a concentric arrangement; some of them are large, others are smaller in size. The number of cell-rows in the sclerenchyma, phloem and cambium of the vascular bundles is given in Table 1.

In the case of the 1 μ g/ml dose the hypodermis shows a considerable change, namely, its width becomes more uniform, and the "undulate" character observed in the control shows a decreasing tendency. As to the size of the vascular bundles, large vascular bundles are in this treatment much more than small ones compared to the control. An examination of the components of the vascular bundle reveals that the number of sclerenchyma cell-rows is sharply reduced, and so is the wall thickness of the sclerenchyma cells compared to the control. A slight increase in the number of phloem cell-rows can be observed, while the number of cambium cell-rows did not change relative to the control (Table 1, Fig. 1).

In response to 5 μ g/ml of MNNG the number of hypodermis cell-rows slightly increased compared to the control. The ratio of small to large vascular bundles is different from that in the control, but nearly the same as in the 1 μ g/ml treatment (Table 1). As for the components of the vascular bundles (Fig. 3), the number of sclerenchyma cell-rows shows a substantial decrease, while in the number of phloem cell-rows a greater- and in that of

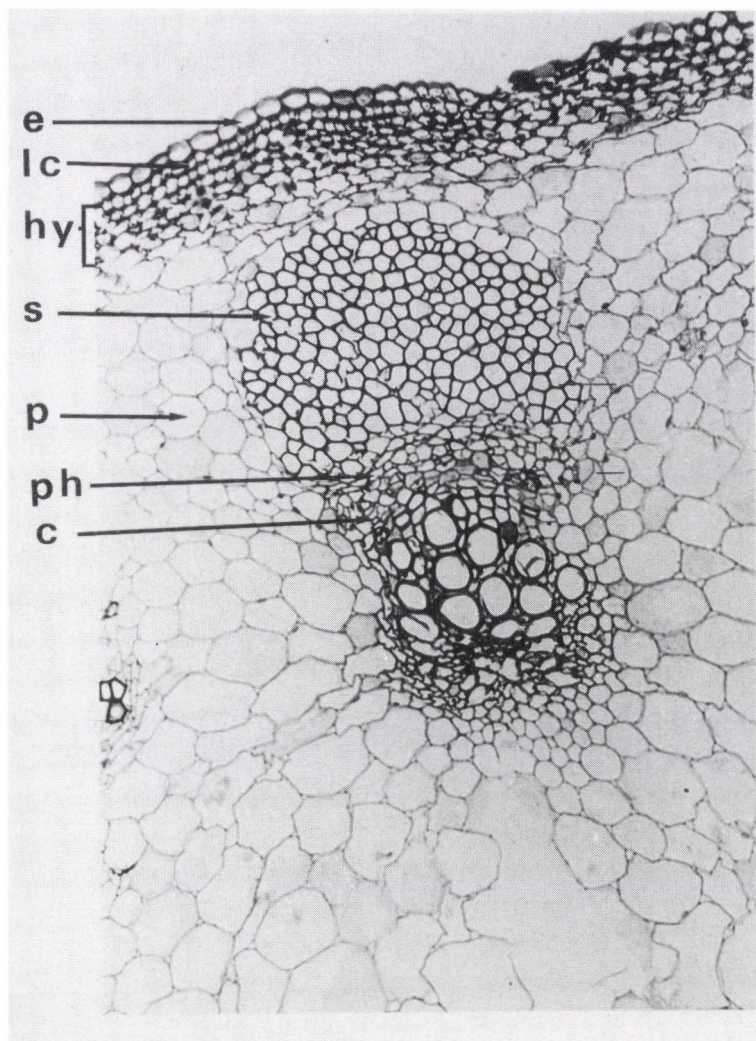


Fig. 3. Part of cross-section with a vascular bundle from sunflower stalk treated with 5 μ g/ml MNNG (e = epidermis, lc = lamellar collenchyma, hy = hypodermis, s = sclerenchyma, p = parenchyma of cortex, ph = phloem, c = cambium) 126x

the cambium cell-rows a lesser extent of increase can be observed (Table 1). The thickness of the sclerenchyma cell-walls was reduced by half in comparison to the control (Fig. 1).

The 10 μ g/ml dose slightly increased the number of the hypodermis cell-rows compared to the control, but relative to the 5 μ g/ml treatment no

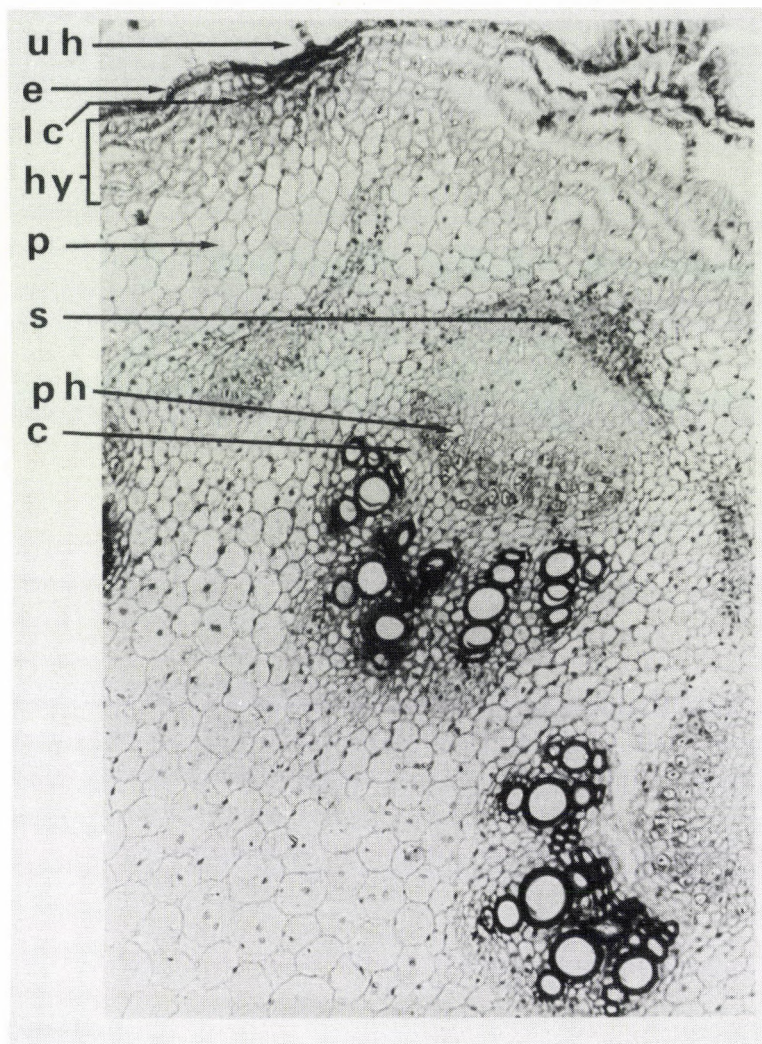


Fig. 4. Part of cross-section with vascular bundles from sunflower stalk treated with 10 $\mu\text{g/ml}$ MNNG (uh = uniseriate hair, e = epidermis, lc = lamellar collenchyma, hy = hypodermis, s = sclerenchyma, p = parenchyma of cortex, ph = phloem, c = cambium) 126x

difference was found. The ratio of small- to large vascular bundles differs from that in the control, but in comparison to the 1 and 5 $\mu\text{g/ml}$ treatments there was hardly any difference (Table 1). As for the components of the vascular bundles (Fig. 4), the number of sclerenchyma cell-rows shows a considerable decrease compared to the control. The number of the phloem

cell-rows increased essentially, while that of the cambium cell-rows to a small extent relative to the control (Table 1). The walls of the sclerenchyma cells became remarkably thin compared to both the control and the 1- and 5 $\mu\text{g/ml}$ treatments (Fig. 1). The cells in the parenchyma of cortex displayed conspicuous proliferation without atypia in comparison to both the control and the 1- and 5 $\mu\text{g/ml}$ treatments.

DISCUSSION

MNNG had a carcinogenic effect on all animal species used for the experiments (mouse, rat, hamster, guinea-pig, dog), and proved carcinogenic in single-application experiments too (IARC Monographs 1974). The MNNG does not require metabolic transformation for its carcinogenic action. Namely, the microsomal enzyme system found first of all in the livers of mammals is absent from plants. MNNG was chosen for its good water-solubility, and because it exerts its effect on plant cells by itself, without metabolic transformation.

In sunflower, as a plant highly responsive to chemicals, we induced tumour-like growth with Dicamba in earlier experiments (HERDI 1986). For the MNNG examinations we chose sunflower because we expected similar effects. Dicamba induced lesions visible to the naked eye — tumour-like growths — on sunflower leaves. In these growths the tissue structure of the leaf was totally different from the normal tissue structure, and out of the components of vascular tissues the tracheides (HERDI 1986) were found in very large numbers. Similar symptoms were observed concerning tumour-like lesions induced in sunflower by BRAUN and STONIER (1958).

MNNG did not induce such lesions in sunflower, but besides damaging the vascular bundles caused reduction of or a slight increase in certain tissue components. As one of the most important results of the experiment, the histological examination revealed intensive cell proliferation induced by the MNNG in the cortical parenchyma, although no tumour-like lesions was visible on the stalk (Fig. 4). The fact that the intensive proliferation did not cause partial or total thickening of stalk was supposedly due to the much smaller size of the proliferating cortical parenchyma cells compared to those in the control (Figs 2 and 4). The histological picture of this tumour-like condition did not show atypia, a characteristic of malignant tumours in mammals, in our case either. Thus, in plants these

substances did not cause cell proliferation involving atypia, i.e. malignant transformation. MNNG caused chromosome aberration in onion (FISKESJÖ 1981) which suggests that it is linked with the DNA of plants as well.

The action of MNNG on animal- and plant cells has the common feature that it can induce cell proliferation, but the basic difference is that while in the case of mammals the proliferation involves atypia, in plants atypia is not found. In this sense the proliferation of plant cells resembles most the benignant tumours of mammals, which show no atypia.

The carcinogenic pesticides are supposed to represent potential danger not only for humans, they may have an unfavourable effect on the development of cultivated plants by inducing some sort of cell proliferation in them.

Finally, the experiment calls attention to the fact that in studies of this nature the light microscope examination of plant tissues may supply highly important information, particularly in cases when there are no visible lesions.

ACKNOWLEDGEMENTS

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REFERENCES

- Allard, R.V., Robert de Rose, H., Swanson, C.F. (1973): Some effects of plant growth regulators on seed germination and seedling development. Bot. Gaz. 109: 13-39.
- Arlt, K., Feyerabend, G. (1982): Herbizide und Kulturpflanzen. Akademie Verlag, Berlin.
- Braun, A.C., Stonier, T. (1958): Morphology and physiology of plant tumors. In: Heilbrunn, L.V., Weber, F.: Protoplasmatologie. Handbuch der Protoplasmaforschung. Springer Verlag, Wien.
- McCalla, D.R., Reuvers, A., Kitai, R. (1968): Inactivation of biologically active N-methyl-N-nitroso compounds in aqueous solutions: effect of various conditions of pH and illumination. Canad. J. Biochem. 46: 807.
- Felber, I.M. (1948): The formation of protuberances on bean leaves in response to 2,4-D treatments. Amer. J. Bot. 35: 555-558.

- Fiskesjö, G. (1981): Benzo(a)pyrene and N-methyl-N-nitroso-guanidine in the Allium test. Hereditas 95: 155-162.
- Fiskesjö, G., Lassen, C., Renberg, L. (1981): Chlorinated phenoxy-acetic acids and chlorophenols in the modified Allium test. Chem.-Biol. Interactions 34: 333-344.
- Herdi, F. (1986): A dicamba tumorképző hatásának vizsgálata a napraforgó (Helianthus annuus L.) levelén (Study of dicamba in causing tumors on leaves of sunflower (Helianthus annuus L.)). (In Hungarian). Növényvédelem, XXII: 14-21.
- Iarc Monographs on the evaluation of the carcinogenic risk of chemicals to man. Vol. 4: 183-195. Lyon, 1974.
- Kiermayer, O. (1964): Growth responses to herbicides. Pages 207-230 in Audus, L.J.: The Physiology and Biochemistry of Herbicides. Academic Press, London-New York.
- Maróti, M. (1976): A Növényi Szövettenyésztés Alapjai (Fundamentals of plant tissues cultures). Akadémiai Kiadó, Budapest.
- Murray, M.A., Whiting, A.G. (1947): A comparison of the effectiveness of 2,4-dichloro-phenoxy-acetic acid and four of its salts inducing histological responses in bean plants. Bot. Gaz. 109: 13-39.
- Pizzolato, T.D., Regehr, D.L. (1981): Anatomical effects of 2,4-DB on tomato internodes. Can. J. Bot. 59: 1749-1760.
- Schaper, F. (1970): Zur Analytik von N-Alkyl-N-Nitrosamiden. Thesis, University of Freiburg/Br.
- Sorokin, H.P., Mathur, S.W., Thimann, K.V. (1962): The effects of auxins and kinetin on xylem differentiation in the pea epicotyl. Amer. J. Bot. 49: 444-454.
- Tukey, H.B., Hamner, C.L., Imhofe, B. (1945): Histological changes in bindweed and sow thistle following application of 2,4-dichloro-phenoxy-acetic acid in herbicidal concentrations. Amer. J. Bot. 35: 555-558.

ULTRASTRUCTURAL CHANGES OF MITOCHONDRIA DURING CELL DEDIFFERENTIATION OF
EXPLANTS

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Electronmicroscope studies of ultrastructural changes of mitochondria during simple stages of cell dedifferentiation. The most markant structural changes mitochondria were observed on the 12th day from begin of inoculation. At this stage of cell growth, two types of mitochondria were present with different number cristae.

INTRODUCTION

Studying dedifferentiation of the cells of higher Plants, more and more attention is paid to studies of ultrastructural organization of the cells of the explant itself, as well as of those of the callus.

During dedifferentiation of plant cells, a metamorphosis of the intracellular organization, structure and function of many cell components are changed. Besides of aberrative changes of the genome (D'AMATO 1964, 1965; KUNACH 1978; NOVÁK 1973; PARTENEN 1963; PARTENEN 1965; SEKERKA 1983, 1984), of the nucleolus (FROLOVA 1981; SEKERKA 1984), and a rigorous rebuilding of the whole membrane system and of other structures (BUTENKO et al. 1967; ISRAEL et al 1966; KORDJUM et al 1980; NEDUCHA 1969; SEKERKA et al. 1983), also mitochondria undergo striking changes playing an important role of an energy donor, which is necessary for all basic processes on cell level in the dedifferentiating cells, size and number of mitochondria, their inner structure, the number of cristae, the density of the matrix and the degree of vacuolization are changed (KORDJUM et al 1980; MARTIN 1970; NEDUCHA 1969). These changes of the single components during cell dedifferentiation are subject of our interest.

MATERIAL AND METHODS

Cells of the primary cortex of the root (prolonging zone) of the horse-bean (*Vicia faba* L.) were used as experimental material, in the dedifferentiation process in in vitro conditions, up to forming of the primary callus. For induction, the nutrient medium according to MURASHIGE-SKODG (1962) was used.

For ultrastructural analysis, samples were taken from the intact tissue, as well as samples of the explant after 1, 2, 3, 6, 10 and 20 days on the cultivating medium.

The samples were fixed in glutaraldehyde and OsO_4 and embedded into Durcupan ACM (Fluka). Ultrathin sections were made by help of the ultra-microtome Tesla BS-490, contrasted by lead citrate for 20 minutes according to REYNOLDS (1963) and investigated by help of the electron microscope Tesla BS-613.

RESULTS AND DISCUSSION

Comparing studies of intact cells with those of the explants during dedifferentiation, show that decisive changes occur in this process. Electronograms obtained from cells of the original tissue show the total ultrastructural appearance of these cells to be similar to those of other types of tissues; they are at different stages of vacuolization, the vacuoles of different size and shape are more or less chaotically dispersed over the whole cell area. In intact cells, occurrence of larger vacuoles can be observed pushing off the cytoplasm with the cell components to the marginal region, where it forms a narrow layer along the wall. Mitochondria are of oval or fairly oblong shape, of different size, the electron density of their matrix is the same as that of the cytosol. The matrix of the mitochondria is often interrupted by electrontransparent sites occupying sometimes a considerable volume of the mitochondria (Fig. 1). The inner membrane system of the mitochondria is weakly differentiated and formed by a small number of short cristae. The perimitochondrial space is approximately equally broad along the whole periphery of the mitochondrion, similarly as the space between the pair of membranes, which form cristae.

As early as after 48 hours of in vitro cultivation (lag phase), the mitochondria in the explant cells undergo fundamental changes. Differentiating of a complicated inner membrane system (increasing of number and length of the cristae), proves the fact that respiration increases already in the lag phase; its energy is deposited in an increased way in the form of ATP, which is later used in increasing proteosynthetic activity of

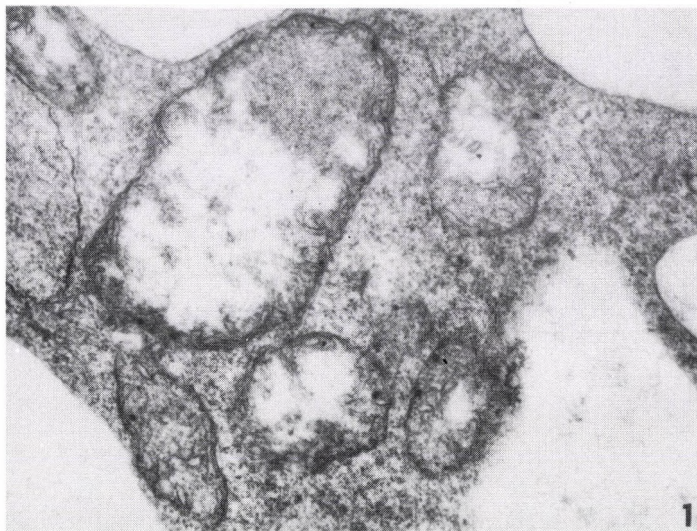


Fig. 1 Mitochondria with a small number of short cristae

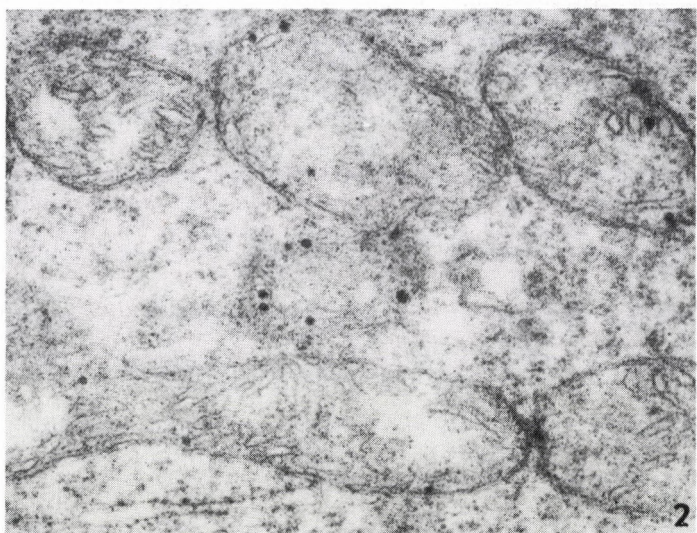


Fig. 2 Transversal division of mitochondria after 48 hours of in vitro cultivation

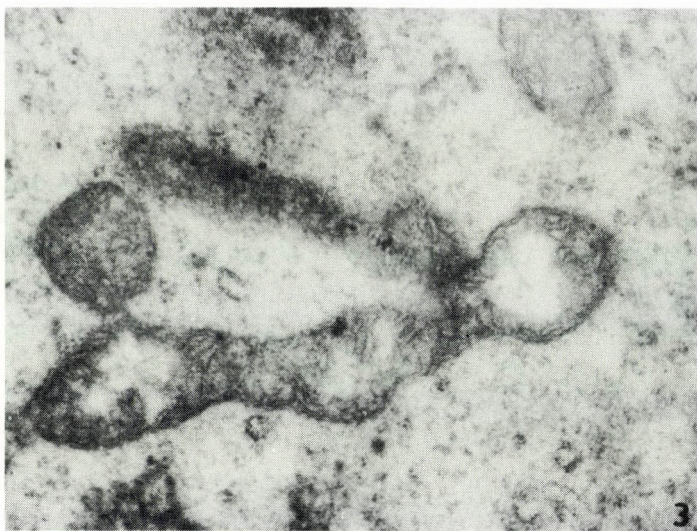


Fig. 3 Division of the mitochondria by constricting and budding



Fig. 4 Mitochondria with a parallel orientation of the cristae to the longitudinal axis of the mitochondrion

the cells and in their reproduction in the exponential phase of callus growth. In the cells, that had entered into reproduction, the size of mitochondria increases, especially in the direction of their longitudinal axis; simultaneously, their total number increases per unit of area. Chains can be often observed, formed by equally oriented mitochondria (Fig. 2). This phenomenon proves an increased reproduction of mitochondria by transversal division. Moreover, also division of mitochondria by constricting or budding occurred (Fig. 3). At the end of the exponential phase of cell growth (on the 12th day from the begin of cultivation) two kinds of mitochondrial populations were found, which differed by their ultrastructural characteristics.

The differences in the structural characteristics of the two occurring populations of mitochondria, concern, first of all, the way of arrangement of the cristae. Whereas the first group is represented by common and most often occurring mitochondria with a chaotical dispersion of the cristae, and with their vertical orientation to the longitudinal axis of the mitochondrion respectively, the second one is formed by mitochondria with a parallel orientation of the cristae to the longitudinal axis of the mitochondrion (Fig. 4).

The space between the membrane pair of the cristae was partially dilated, the matrix was of much higher electron density than the cytosol. The arrangement of the cristae in the inner part of the mitochondrion was not uniform. Whereas 2/3 of the large volume of the mitochondrion had a high amount of cristae, the remaining part did not form any cristae. An analogical picture was shown also on electronogram 5, illustrating a mitochondrion in the stage of division by constricting, where both the halves differ by the presence of cristae. Occurrence of dumb-bell like mitochondria is a prove for increased reproduction of these components. In some cells, besides the two mentioned types of mitochondria, in rare cases, also the presence of mitochondria was observed with symptoms of a concentrical arrangement of the cristae. As it is well known, such a type of mitochondria is characteristic for cells with high metabolic activity.

The most striking changes of cell mitochondria, observed at the end of the exponential phase of growth, are in accordance with the works of (NEDUCHA 1969; MARTIN 1970), who studied these changes on parenchymatic cells of carrot and pea roots.

Moreover, the ultrastructural characteristic can change together with the size and number of mitochondria, also as a consequence of cyto-

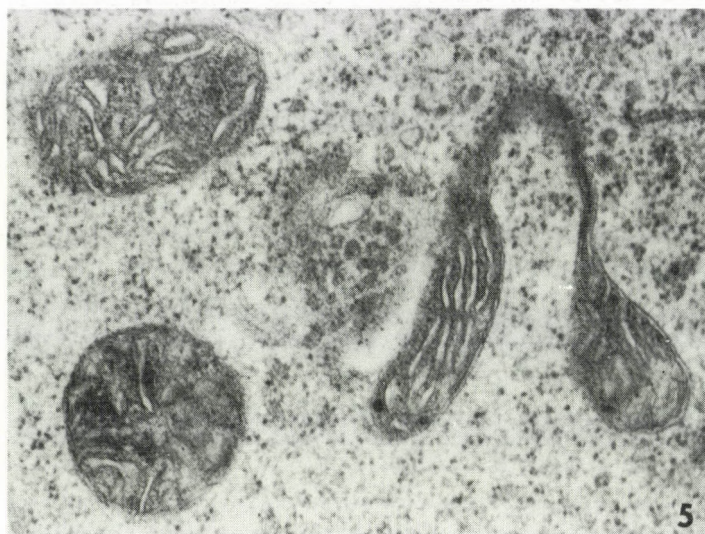


Fig. 5 . Mitochondria in the stage of division by constricting — both the halves differ by the presence of cristae

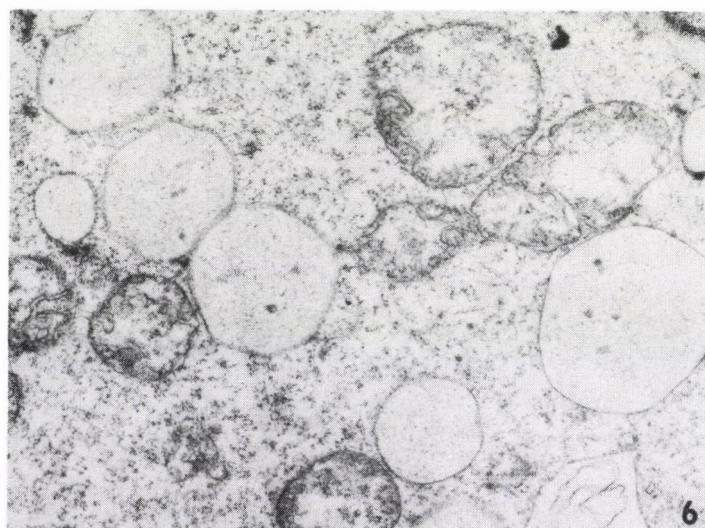


Fig. 6 Mitochondria in different states of destruction

genetic changes within the transforming cells and callus cells. It is, first of all, the question of arising polynucleic cells and of cells at different degrees of ploidy (NAGL 1978). During the stationary phase of the callus cells (14th to 18th day after inoculation), the mitochondria increase their volume, stabilizing their size and decreasing polymorphy of their shape to the end of the stationary phase.

With respect to the fact that the growing callus represents a rather heterogeneous cell mass after two to four weeks of cell cultivation, also a whole scale of changes in the ultrastructural characteristics of mitochondria can be observed in the single cell types.

Striking structural changes are undergone by the mitochondria in the cells of protracheal elements, which begin to differentiate on the 14th day from the begin of inoculation. As a consequence of intensive vacuolization and of the differentiation of the central vacuole, mitochondria are localized in the peripheric layer of the cytoplasm along the cell wall, either isolatedly or in groups. Besides mitochondria with a normal ultrastructural organization, a well preserved membrane envelope, cristae and matrix, also mitochondria at different stages of destruction can be seen in their neighbourhood. We suppose that it is the question either of older not functioning mitochondria, or of mitochondria yet in function, the destruction of which is caused by programmed autolysis of the inner content of the cells in question, during their morphological and functional specialization.

Characteristic features of destruction changes of mitochondria, there are: fragmentation of the membrane envelope, dilatation of the inner space of the cristae and an increase of the elctrontransparence of the matrix, with local or global vacualization of the mitochondria as a consequence (Fig. 6).

REFERENCES

- Bobák, M., Sekerka, V. (1988). Ultrastructural changes of nuclei in parenchymatic endosperm cells during the dedifferentiation process. (In press).
- Butenko, R.G., Jakovlev, Z.M. (1967): *Izmeneniye tonkoy struktury kletok parenchimy steblya tabaka pri dediferenciatsii v kulture in vitro.* In: *Materialy 11. vsesoyuz. simp. po primeneniyu elektron. mikroskopii v bot. issled.* Kiyev, 44.
- D'Amato, F. (1964): Endoploidy as a factor in plant tissue development. *Caryologia*. 17: 31.

- D'Amato, F. (1965): Endoploid as a factor in plant tissue development. Symp. Plant Tissue Culture. Penna. In: White, P.R., Ed. McCutchan Publ. Corp. Berkely, 449.
- Frolova, L.V. (1981): Osobennosti populyatsiy kultiviruyemykh kletok. In: Kultura kletok rasteniy, Butenko, R.G. (ed.) Moskva: Nauka. 5.
- Israel, H.W., Steward, F.C. (1966): The fine structure of quiescent and growing carrot cells, its relation to growing induction. Ann. Bot., G. Brit. 117: 63.
- Kordjum, E.L., Neducha, E.M., Sidorenko, P.G. (1980): Strukturnofunkcional'naya Charakteristika Rastitel'noy Kletki v Procesoch Dediferencirovki i Diferencirovki. Kiyev: Naukova dumka. 111. pp.
- Kunach, V.A. (1978): Citogeneticheskaya i morfologicheskaya izmenchivost' shtammov kul'tury tkaney haplopappusa v protsesse ich formirovaniya. In: Kultura kletok rasteniy. Kijev: Naukova dumka. pp. 108.
- Martin, G.G. (1970): Formirovaniye struktury mitochondriy v protsesse rastu rastlinnich kletok. Dop. An USSR, ser. B. 21: 1032.
- Murashige, J., Skoog, F. (1962): A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plantarum. 15: 473-497.
- Nagl, W. (1978): Endoploidy and polyteny in Differentiation and Evolution. Amsterdam, North-Holland. 283. pp.
- Neducha, E.M. (1969a): Izuchenie plastid i sodержanie krachmala v kletkach kul'tury tkani morkovi in vitro. Citologia. 2: 219.
- Neducha, E.M. (1969b): Izuchenie metamorfoza plastid korneploda morkovi v kul'ture in vitro. Dis. kand. nauk. In: Kordjum, E.L., Neducha, E.M., Sidorenko, P.G.: Strukturnofunkcional'naya charakteristika rast. kletki v procesach diferenc. a dediferencirovki. Kiyev: Naukova dumka 1980. pp. 111.
- Novák, F.J. (1973): Karyologické studium kultur rostlinných explantátů in vitro. In: 1. Kolokvium využití kultur rostl. explantátů in vitro v genetice a šlechtění. Olomouc, 19. pp.
- Partenen, C.R. (1963): Plant tissue in relation to developmental cytology. Int. rev. Cytol. 15: 215.
- Partenen, C.R. (1965): Cytological behaviour of plant tissues in vitro as a reflection of potentialities in vivo. In: Proc. Int. Conf. Plant Tissue Culture, White, P.R. (ed.), Penna State Univ., McCutchan Pub. Corp., Berkeley, 463. pp.
- Sekerka, V. (1983): Aberrant changes in the genome of cells of epicotyl in Vicia faba L. in the process of dedifferentiation. Acta F. R. N. Univ. Comen. Genetica XIV: 13.
- Sekerka, V. (1984): Influence of 3-metoxycarbonylmethylbenzothiazolium-bromide on growth and mitotic activity of Vicia sativa L. roots. Acta Soc. Bot. Polon. 1: 53.
- Sekerka, V., Bobák, M. (1983): Ultrastructural changes of the parenchymatic cells in the endosperm during dedifferentiation of Vicia faba L. Acta F. R. N. Univ. Comen. Physiologia Plantarum XIX: 27.

Street, H.E., Davey, M.R., Sutton-Jones, B. (1962): Ultrastructure of plant cells growing in suspension culture. In: Ultrastructural features of cells and tissues in culture. Simpos. Biol. Hungarica, Budapest, 14: 145.

Venable, J.M., Coggeshall, R. (1965): A simplified lead citrate stain for use in electron microscopy. J. Cell Biol. 25: 407.

BOOK REVIEWS

ed.: G. FEKETE

MARGARIS, N.S., ARIANOUTSOU-FARAGGITAKI, M. and REITER, R.J. (eds). Adaptations to Terrestrial Environments. Plenum Press. New York and London 1983, pp. 247.

This volume contains 17 selected papers of the International Symposium on Adaptations to Terrestrial Environment, held in Halkidiki-Kriopogi, Greece, between September 26 - October 2, 1982.

The papers deal with a great variety of species from insects to mammals. The authors are successful in providing a well-balanced treatment of physiological and biochemical problems of adaptations to terrestrial environment.

The volume is divided into two parts: Invertebrates and Vertebrates. The first part contains papers about the adaptations of invertebrates to terrestrial first part.

The aim of the paper entitled "limiting similarity in rove beetles (Col. Staphylinidea) of habitat inland" is to examine resource utilization of rove beetles and to test whether species niches are overdispersed.

The approach on staphylinid organization and niche segregation suggests that species are predisposed to different niches and they will diverge separately as they evolve.

The next paper deals with low temperature-induced diapause still extant in a new tropical species of leptopilina (Leptopilina boulandi) which is a larval parasitoid of Drosophila melanogaster.

The third paper gives an overview of cold tolerance in Canadian arctic insects. Nine species of insects from different geographical regions of Canada were examined for freezing tolerance, supercooling capacity, water contents and change in biochemical characteristics during acclimation to subzero temperatures.

The major conclusion is that the examined species have different adaptations to low temperature survival, even if they fall within one or other of the two major overwintering strategies.

In the next paper, a description of the seasonal activity of soil fauna (as well a macro- and micro-fauna) in a phryganic (east Mediterranean) ecosystem is provided.

Paper 5 entitled "Comparative studies of Orthopteran species adapted to living on the ground and of some fliers from the same order" gives an account of the behavior of some orthopteran species, found in wheatfields and the bush surrounding them, from the point of their moving (excellent runners, good jumpers and strong fliers). In all the examined three species (Decticus albifrons, Calliptamus sp., Acrida mediterranea) a strong morphological and anatomical adaptation can be found in close connection with their behavior and their environment. The following paper deals with the symbiotic adaptation between cynipids and their host-plants, from the point of view of coevolution.

The next study "Adaptation of gall mites (Acari, Eriophyoidea) to live in galls" deal with the structure of gall mite mouthparts and of feeding punctures left on the host plant, based on two examples: Eriophyes cladophthirus and Phytopus padi Nal. The excellent micrographs greatly support the examinations.

The last paper in Part One gives an overview of adaptation between the gall maker and its host-plant. Bud galls are in the front of this

study, but we can also find some information about the biology of cecidozoa.

Part 2 provides information on adaptations of vertebrates to special environmental factors (light, temperature). Furthermore, it also deals with behavioral, physiological and biochemical problems.

There are nine papers in this part. They deal with the occurrence of altruism, the central problem in the understanding of social behavior.

There are three main approaches to the analysis of the evolution of altruism, which are based on "inclusive fitness, population genetic analysis and the evolutionary game theory". We can get original concept and useful new information about the models for altruistic warning, linear fitness combination and evolutionary game theory and combinatorial models in diploid species, too.

The aim of the following paper is to point out the most common synergistic interactions between behavioral and morphological antipredator adaptations of terrestrial salamandra species and the evolution of these sets of adaptations. It is well-supported with beautiful photos.

The third study entitled "The inter-nesting interval of zakynthos loggerheads" deals with the methods and the results of a long-term tagging program on the sea turtle Caretta caretta (L.): an estimation of the inter-nesting interval.

The next study is concerned with the reproduction strategies in birds of the tropics. The authors' purpose with this review is to show that in keeping with the characteristic diversity of tropics a variety of strategies have been adapted to timing reproduction as well as to ultimate factors, proximate factors.

The fifth paper deals with nutritionally related metabolic adaptations of carnivores and ruminants.

It is divided into two subchapters: The first gives us useful information about adaptations associated with energy and protein metabolism, the second deals with vitamins, taurine and essential fatty acids.

The examples indicate that the metabolic pathways of the ruminants and true carnivores have adapted to peculiar end products of their digestive system.

The following study deals with the activity of superoxide dismutase in the rat exposed to extreme environmental conditions. The authors examined the effect of acute and chronic exposure to low temperatures and to effect of X irradiation. It can be concluded that superoxid dismutase plays an important role as a protector agent against the extreme environmental conditions such as the above mentioned cold and X-irradiance effects.

The paper entitled "Adaptations of the reproductive system of rodents to changing photoperiodic conditions" briefly summarizes the mechanisms whereby the light dark cycle determines the functional status of the reproductive system of the rodents.

The study deals with the conversion of photoperiodic information into a hormonal signal and the reproductive consequence of the pineal gland.

The eighth study gives us information about the endocrine cycles and hibernation in the hedgehog and the mechanisms of adaptation to natural variations in the environment.

We can get some useful new information about the seasonal variations in locomotor activity and in body weight, in cortico-adrenal and thyroid activity. Furthermore, it summarizes the seasonal variations in the testicular function.

The title of the closing paper in the volume is "Comparative mechanisms of physiological, metabolical and eco-ethological adaptation to the winter season in two wild european mammals: the european badger (Meles

meles L.) and the red fox (*Vulpes vulpes* L.)". In this work the authors considered two essential physiological functions: the testicular and the thyroid function in these mammals. On the basis of their results it is established, that red fox is characterized by a greater plasticity and it shows a greater adaptability to the environmental factors than badger.

The whole volume is a well-prepared and documented work, especially Part 2. It is supplied with author, systematic and subject indexes.

The book may be recommended to everybody dealing with environmental-adaptation biology.

Z. TUBA

Franz-Chirstian CZYGAN (ed.): *Pigments in Plants*. 2nd revised and enlarged edition. Gustav FISCHER Verlag, Stuttgart. New York 1980, pp. 447, 139 figures, 29 tables.

This second edition of the book came out because of the great interest of biologists. This new edition contains not only the results of the expansion of old chapters, but also presents the current state of pigment researches.

The volume includes 19 papers with 139 figures and 29 tables, well-selected references at the end of each chapter, a detailed subject, author and scientific names index.

The first chapter entitled "Light and Pigments" (H. MOLER) deals with the problem of the extent to which synthesis and contents of pigments are regulated by light. As an experimental subject, *Sinapis alba* seedling was chosen.

In the further parts of the chapter, the phytochrome system, the phytochrome control of Chlorophyll b formation and of anthocyanin formation, the light control of anthocyanin formation in the mesocotyl of *Sorghum vulgare* are discussed. At last the general significance includes theoretical and practical aspects of the investigations. From the view of the theoretical aspect it is important that control of mass pigment synthesis by the sensor pigment phytochrome is an integral part of photomorphogenesis.

The practical aim of these researches is to predict the best combination of photomorphogenic lighting for producing a desired crop in a given time at minimum cost.

The second paper gives an account of carotenoid biosynthesis (Brian H. DAVIES). After a short introduction, the structure and nomenclature of carotenoids are described, as well as their structure reflecting their mode of biosynthesis.

In studying the biosynthesis of carotenoids, they used the more direct isotope method. It can be concluded from the results that the general features of carotenoid biosynthesis are essentially the same in higher and lower plants.

Then the most important steps are discussed, such as early steps, up to C_{20} , formation of the first C_{40} hydrocarbon, and phytoen, formation of phytoen, triterpenoid carotenoids (C_{30}), formation of alicyclic carotenes, and C_{45} and C_{50} homocarotenoid, aromatic carotenes.

In subchapter 3.8 the aspects of the control of carotene formation in *Phycomyces* is discussed.

Finally, the paper deals with C_{40} xanthophyll formation and with the partially degraded carotenoids. At the end of the partially degraded

carotenoids. At the end of the study, an appendix can be found beside the rich list of references.

The following chapter discusses the molecular mechanisms and possible functions of the reversible light-dependent xanthophyll conversion (Xanthophyll cycle) in the metabolism of the chloroplasts. We can get a very good overview about the general characteristics of the xanthophyll conversions, distribution of the xanthophyll-cycle in the plant kingdom, induction of the violaxanthin deepoxidation in isolated chloroplasts, mechanism of zeaxanthin formation, activation of the deepoxidase enzyme in intact cells, regeneration of the deepoxidation reductant, epoxidation in whole leaves and in isolated chloroplasts. Furthermore, this review pays attention to the interdependence of the reaction partners of the xanthophyll cycle, and also localization of the enzymes of this cycle in chloroplasts.

The greatest merit of this paper is that these results have provided new insight into the molecular mechanism of the xanthophyll cycle.

In the study entitled "Photoregulation of carotenoid biosynthesis: an example of photomorphogenesis" briefly summarizes the mechanism of photomorphogenesis in general, especially the "blue-light" induced biosynthesis of carotenoids in fungi. On the basis of the investigations it can be suggested that the mechanism of photoinduction of carotenoid biosynthesis in fungi involves photoregulated differential gene activations. One of the most interesting new results is found in the following review, which deals with the treatment of the role of algal carotenoids as taxonomic-systematic markers. The most important conclusion is that the individual algal carotenoids can be useful to the taxonomists, but these are frequently relevant only in lower taxa; the phylogenetic tree of the algae only on the basis of the pigment (mainly carotenoid) distribution can not be exact.

The paper entitled "Chromoplasts" is a detailed survey of this principal carotenoid bearing cell organelle which also serves an important ecological function.

The study deals with chromoplasts and gerontoplasts, with their fine structure, biochemistry, development and at last with the phylogenetic aspects of these organelles. After the brief summary, the study is completed with some new information.

The following review deals with the occurrence and distribution of terpenoids, especially diterpenoid pigments in plants. It gives a list of the more important chromophoric systems, then describes the known terpene structures, and diterpenoid pigments in more detail.

The next chapter gives an account of flavonoid biosynthesis, including the role of chalcone isomerase, biosynthesis of anthocyanins, flavonoid methyltransferases, and regulation of flavonoid biosynthesis.

The study entitled "Degradation of Flavonoids and Isoflavonoids" describes some aspects of their metabolism in higher plants in order to document the principles of the degradation of aromatic and heterocyclic plant constituents in the producing plants.

The following paper tries to draw attention to the current importance of flavonoids as chemotaxonomic markers in plants. It deals with the plant kingdom first, then with the flavonoids as taxonomic and evolutionary markers in higher plants.

One of the longest and most detailed chapters deals with chlorophyll biosynthesis enzymes and the regulation of enzyme activities. It begins with the distribution of chlorophylls and the intermediates of their biosynthetic pathway. The most comprehensive part of the chapter gives a very good overview of the enzymes taking part in the biosynthetic pathway of chlorophyll. In the remaining two subchapters, the localization and size of synthesis of chlorophyll formation enzymes and the regulation of chlorophyll biosynthesis are discussed.

The next chapter deals with the biological degradation of chlorophyll in senescent plant tissues.

The following study discusses plant biliproteins as well as phyco-biliproteins and phytochrome. We can get some information about their structural organization, their linkage to the protein, their biosynthesis and regulation.

In the paper entitled "Quinonoid pigments" we can read about the structure, the biosynthesis, degradation and biological activity of these pigments. On the basis of the results it is suggested that quinonoid pigments may be advantageous to plants in the resistance to insects.

The next study discusses the chemistry of betalains (betacyanins, betaxanthins), their occurrence in the mushrooms, and the role of betalainic acid and muscaflavin. At last it deals with the formation of betalain and cAMP and related taxonomic problems.

The closing study deals with the pigments of higher fungi (Macro-mycetes). We can get an overview of the pigments of shikimate pathway, the pigments of acetate malonate pathway, the pigments of mevalonate pathway. Finally, it deals with the nitrogen-containing pigments.

Summing up what has been said, this is a well-supplied, excellent volume with a nice layout and several recent results. It can be highly recommended primarily for those dealing with this field of biochemistry, but also for every plant physiologist and student interested in plant biochemistry and physiology.

Z. TUBA

Walter LARCHER: *Ökologie der Pflanzen auf physiologischer Grundlage*. 4., Überarbeitete Auflage, Verlag Eugen ULMER Stuttgart, 1984. 181 Abbildungen, 54 Tabellen, pp. 403.

This revised 4th edition of the book provides an extremely good up-to-date overview of physiological plant ecology. It can be said that with the appearance of the first and further editions of this volume a wide gap has been filled in plant ecology. In the fourth edition, the author has taken into account the requests and critical comments of users and readers of the previous editions (published in German and English).

The principal aim of the volume is to convey the conceptual framework upon which this discipline is based, to offer insights into the basic mechanisms within the system "plant and environment" and to present information and examples of current problems in their rapidly developing area.

This volume is enlarged with two new chapters "Plants and Ecosystems" and "Nitrogen Budget (Utilization and Cycling of Nitrogen)". The chapters on "Carbon Budget" and "Water Relations" have been expanded considerably. However, the subchapter "Pollution Injury" of the previous edition, the ecophysiology of tropical plants and of plants growing in arid regions has been more strongly emphasized and the environmental influences on growth and development are not as detailed as those affecting metabolism.

The volume consists of 8 chapters, on 403 pages with 181 figures and 54 tables. Before the first chapter we can find the list of abbreviations, symbols and conversion factors which promotes our orientation when reading the text.

The chapters are as follows:

1. The Environment of Plants
2. Plants of Ecosystems
3. Radiation and Temperature: Energy, Information, Stress
4. Carbon Utilization and Dry Matter Production
5. Utilization and Cycling of Nitrogen
6. Utilization and Cycling of Mineral Elements
7. Water Relations
8. Synopsis

Finally, the literature and subject index are presented.

The first chapter (Die Umwelt der Pflanzen) is the shortest of all. It gives a brief account of the environment of plants (the hydrosphere, the atmosphere, the lithosphere and the soil). In the last part of the chapter we can read about the so-called ecosphere, a part of the earth which supports life.

The 2nd chapter (Die Pflanze im Ökosystem) describes the concept of ecosystem, mass and energy transfer of ecosystems. Afterwards the author deals with the information transfer and regulation of ecosystems, with biotic interference effects and with abiotic stress effects within ecosystems.

Chapter 3 deals with radiation and temperature: energy, information and stress (Strahlung und Wärme: Energie, Information, Belastung). 3.1 is about radiation. Relatively small amount of radiant energy gives the latent chemical energy used by the photosynthesis, larger fraction is transformed into heat and part of this fraction is used in the evaporation.

3.1.1 deals with radiation within the atmosphere including the attenuation of radiation by the atmosphere and the distribution of radiation in the plant cover.

In connection with the uptake of irradiation by plants we can read about reflection, absorption, and transmission.

3.1.3 is devoted to radiation and plant life. It deals with the direct effects of radiation, e.g. photoenergetic, photocybernetic and photodestructive effects and with the adaptation of plants to the local radiation climate. The main kinds of adaptation are modulative, modificativa and evolutive.

3.2 gives an overview of the role of temperature. 3.2.1 deals with the energy budget including radiation balance, the source of thermal energy, the thermal balance of the plant cover (the radiation balance Q_r ; the energy turnover in metabolite processes Q_M ; heat storage by the phytomass Q_p ; heat storage in the soil Q_{soil} ; exchange of energy with the environment Q_H and Q_E convection Q_E evaporation) and the thermal climate of plant stands.

3.2.2 contains the summary of effects of temperature upon the vital processes of plants such as life-supporting range and functional range. The next part is about the temperature limits for plant life. It gives an account of the temperature extremes; on the Earth, the limits of existence and the capacity to survive, the temperature stress effects and cell death by heat and cold, and temperature resistance. It deals with many different ways of constitutional types of heat and cold resistance of plants. The chapter also includes the resistance differences within populations and the evolution of frost hardening processes.

Subchapter 3.3 gives us detailed summary of the periodically varying environmental factor which is the consequence of the rotation and revolution of the Earth.

It deals with the climatic rhythms such as diurnal variation, seasonal variation; activity rhythms, synchronization of the growth and climatic rhythms. Phenological data, the sequences of phenophyses in the

temperate zone and the tropics are introduced. Finally, some information on the importance of phenometry data is provided.

In chapter 4 (Der Kohlenstoffhaushalt), the author presents information about carbon metabolism in the cell, CO_2 exchange in plants, the carbon budget of the plant, and the carbon balance of plant communities.

Part 4.1.1 entitled "Photosynthesis" discusses bioenergetic and biochemical aspects of photosynthesis, but especially with respect to their ecological importance. It deals with photochemical processes, fixation and reduction of carbon dioxide.

4.1.2 deals with the mechanism of photorespiration. Furthermore it is emphasized that the process of glycolate pathway has not yet been understood in detail.

4.1.3 deals with the mechanism of catabolic processes where the substances are broken down to provide energy for the various metabolic functions of the cells.

The following subchapter discusses the CO_2 exchange in plants. First of all the exchange of carbon dioxide and oxygen as a diffusion process is discussed. After dealing with the diffusion rate and the concentration gradient, we can get some information about the diffusion pathways and transfer resistances in the leaf, the regulation of gas exchange by the stomata (the stomata are the plants control CO_2 entry into the leaf and the release of water vapour). The author summarizes the mechanisms of stomata opening, stomatal movement, the control of this movement and discusses those factors which influence the pore width.

Furthermore, we can get information about photosynthetic capacity and specific respiratory activity, especially the activity of mitochondrial respiration. Then it treats the photosynthetic efficiency coefficient. In the following parts, the influence of developmental stage and activity state upon respiration and photosynthetic capacity are discussed in detail, as photosynthetic capacity and respiratory activity are characteristic of a plant species, but they are not constant.

Since the CO_2 exchange is influenced by a number of external factors, the author deals with the dependence of net photosynthesis on light, the temperature dependence of net photosynthesis and respiration. Furthermore, CO_2 exchange and mineral nutrition, the interaction of external factors affecting CO_2 exchange are discussed in a very clear style. In connection with the gas exchange balance the daily course and annual course of the gas exchange balance, green and non-green components of the plant mass and the overall CO_2 balance are discussed.

The next subchapter deals with the carbon budget of the plant: the author gives attention to the dry matter production, the utilization of photosynthetic products and the rate of growth (planktonic algae, annual plants, perennial herbs, trees) and the translocation of photosynthetic products.

The next part contains a very good review of the carbon balance of plant communities. It deals with the productivity of stands and plants, carbon balance in plant communities according to the production equation, the proportion of the losses due to respiration, loss as detritus and by grazing and their effect on the carbon budget of plant communities. Finally, in this chapter we can get information about the net primary production of the Earth's plant cover, energy conversion by vegetation, the role of plants in the carbon cycle of the Earth and about the oxygen cycling.

In chapter 5, the author pays attention to nitrogen utilization and metabolism as well (Der Stickstoffhaushalt). The first part of the chapter describes the nitrogen metabolism of higher plants including the nitrogen uptake, N-assimilation, N-distribution in the plant, N-excretion.

In the next part, the nitrogen utilization and cycling of micro-organisms is discussed, such as microbial uptake, fixation, excretion, deposition and mobilization of nitrogen. Finally, the author deals with the nitrogen cycling of ecosystems and with the role of plants and micro-organisms in the nitrogen cycling of Earth.

The 6th chapter discusses the utilization and cycling of mineral elements (Der Mineralstoffhaushalt). In this area little experimental research has been done on the specific needs of wild plants.

The subchapter "The soil as a nutrient source for plants" deals with the mineral nutrients in the soil, gives us information about the adsorptive ion binding and ion exchange in the soil, the pH of the soil relating to the connection of soil pH and availability of nutrients.

The following subchapter discusses the role of mineral nutrients in plant metabolism: the uptake of mineral nutrients, the translocation and transport of them, the utilization and deposition of minerals in the plants and the elimination of minerals.

In the part "Habitat-related aspects of mineral metabolism" we can get a good account of calcicolous and calcifugous plants and of plants of saline habitats: useful information on habitat characteristics, the effects of high salt concentrations on plants, salt resistance and regulation of salt content in halophytes is given. The main ways of this regulation are salt filtration, elimination and succulence. Then, a very interesting topic is discussed: how plants behave on soils rich in heavy metals.

In the following part a very dangerous recent problem, the anthropogenic toxic effect on plants is discussed.

Finally, the mineral balance of plant communities and mineral circulation of ecosystems are discussed. The 7th chapter deals with the water relations (Der Wasserhaushalt). First of all this part discusses the main characteristics of poikilohydric and homoiohydric plants. Then, interest is centred on water relations of the plant cell. Water in the cell (water of hydration, stored water), the water potential of plant cells, water potential and the cellular translocation of water, are discussed in the next subchapter.

The most comprehensive part of this chapter deals with absorption, transpiration and water balance in the plant.

Direct water uptake by thalli and shoots, water uptake from the soil, water translocation, water loss from plants and guttation are discussed. The part about water loss is more detailed than the previous ones.

Then, the chapter deals with general water balance and water balance during drought, drought resistance which is the capacity of a plant to withstand periods of dryness. This latest subchapter discusses drought-evading xerophytes, desiccation avoidance, desiccation tolerance, specific survival time and relative drought index.

The last part of the 7th chapter deals with water economy in plant communities, including the water balance equation, available precipitation, evapotranspiration from a stand, runoff and percolation and additional water supplies to the plant cover. Finally, we can get a very good picture about the water budget of the Earth and its importance in the Earth's vegetation.

The last chapter summarizes considerations according to EVANS (1972), special features of ecological methodology and at least data synthesis, ecological models and computer simulation.

The volume contains 181 figures and 54 tables of high standard, facilitating easy comprehension of the book.

The really extensive bibliography contains almost 560 items.

As demonstrated above, this book comprehends all fundamental, adequate and up-to-date aspects, results of modern physiological plant ecology and it contributes greatly to the understanding of the dynamic interactions between environmental factors and plants, the adaptations and reactions of the organisms and their regulation mechanisms.

The book is written in a lucid, simple style and its typographical layout is also to be praised.

That is why the book of professor LARCHER is highly recommended for every ecophysiological and ecologist, but for plant physiologists, agricultural and forestry researchers and for university students, too. This valuable book should not be absent from the botanical libraries.

Z. TUBA

CREASY, L.L. and HRAZDINA, G. (eds): Cellular and Subcellular Localization in Plant Metabolism. Recent Advances in Phytochemistry. Vol. 16. Plenum Press. New York and London 1982, pp. 277.

This volume contains specifically selected papers presented at the Symposium on the Cellular and Subcellular Specialization in Plant Metabolism during the Annual Meeting of the Phytochemical Society of North America, held at Cornell University, Ithaca, N.Y., on August 10-14, 1981.

The present book, published as the 16th volume of the well-known series "Recent Advances in Phytochemistry", provides a very good up-to-date review of specific metabolic interactions of plant cells, cellular and subcellular metabolic specializations. It deals especially with the role of the vacuoles, the nature of the cyanide-resistant respiratory pathway in plant mitochondria, the metabolism in plant peroxisomes, the role of microtubules in plant cell wall growth, the photosynthetic carbon metabolism in chloroplasts, in guard cells of stomata, the C_4 leaf metabolism and with cyanogenic glycosides.

The volume contains eight papers divided into eight chapters.

The first chapter deals with the role of the vacuole (written by George J. WAGNER).

In the introduction, a description is given on the most important roles of cell vacuoles (listed in Table 1) and on the primary and secondary plant products accumulated in plant cells.

In the next part, the current problems of methods for isolating mature plant cell vacuoles and for estimating vacuole/extravacuole solute distribution in tissues after isolation of vacuoles are discussed.

The following parts of this chapter deal with the accumulation of organic acids, ion content of vacuoles, compartmentation of vacuole/extravacuole enzymes, especially with enzymes taking part in flavonoid biosynthesis, and mechanism of tonoplast transport. The research of these latest topics are in a preliminary stage, but the development of vacuole isolation methods in higher plant tissues should facilitate the investigations in this direction.

Chapter two entitled "The nature of the cyanide-resistant pathway in plant mitochondria" written by James N. SIEDOW, deals with plant mitochondrial electron transfer, the occurrence of the cyanide-resistant pathway, inhibition of this pathway, branch point of the pathway, discussing in detail what is currently known about this path and cyanide-resistant oxidase.

Furthermore, it surveys trivial explanations for this pathway, and the results make it clear that reduction of oxygen and the linked oxidation of TCA cycle substrates take place also, that is why more care must be taken regarding these biochemical events.

Chapter three gives an excellent account of "Metabolism in plant peroxisomes" (by Anthony H.C. HUANG). It is divided into the following sub-chapters: introduction, concepts of peroxisomal functions and metabolism, peroxisomes in higher plants, peroxisomes in fungi, algae, perspective and future research on peroxisome metabolism.

The introductory part deals with peroxisomes (microbodies) in general and with their isolation.

The next part gives a brief account of the main peroxisomal functions, such as: compartmentalization of H_2O_2 - producing oxidases and catalases, confirming together enzymes for the production and consumption of glyoxalate.

The following two sections describe the metabolism in the various types of peroxisomes in higher plants and microorganisms, fungi and algae.

Moreover, we can also find many important figures containing the schemes of the different pathways and four excellent electron micrographs.

There is a good review on "the role of microtubules in plant cell wall growth" in chapter 4 (by Myron C. LEDBETTER).

The paper deals with the cell surface and the limiting membrane, the cortical cytoplasm, and the relationships between microtubule-plasmalemma. The text is supplemented with drawings and scanning electron micrographs of high standard.

In chapter 5 entitled "Photosynthetic carbon metabolism in chloroplasts" (by Steven C. HUBER), a description is given on the regulation by inorganic phosphate, the induction phenomena and enzyme activation, the stromal pH and cation fluxes, the chloroplasts and cellular metabolism. The reader can learn that the pH of the chloroplast stroma plays an important role in the regulation of photosynthesis, the enzyme activation may be partly regulated by the metabolite levels.

In the 6th chapter a detailed survey of "Carbon metabolism in guard cells" is given (by William H. OUTLAW), such as malate accumulating, accumulation and synthesis of other organic anions, the changes of carbohydrate concentration and the fate of guard cell malate content during stomata closure. There are many figures and tables facilitating the easy understanding of the up-to-date concepts and results.

The following chapter (7) deals with "cellular aspects of C_4 leaf metabolism" (by W.H. CAMPBELL). The author gives a very good account of the anatomy of C_4 leaves and chloroplasts and protein complement of C_4 cell types. Furthermore, he deals with carbon, nitrogen and sulfur metabolism in detail. The paper contains useful and detailed information about the cellular specialization and the resultant cellular cooperation of C_4 metabolism.

The closing chapter of the volume deals with "the synthesis, storage and degradation of plant natural products, especially with cyanogenic glycosides in *Sorghum bicolor*" (written by Adrian J. CUTLER and Eric E. COHN). The biosynthesis (general features and metabolic channelling) are in the focus of the review. The studies on the metabolism of cyanogenic glycosides have revealed compartmentation at three levels: at tissue, at subcellular and at molecular level. It is hoped, that the results of cyanogenic glycosides research obtained on sorghum will provide a useful model of other higher plant natural products.

Summing up what has been said, I think this book is a valuable, important review of cellular and subcellular localization of plant metabolism. These papers represent the new wave of investigations in this field.

This volume of 277 pages is supplemented with 30 tables, 46 figures and 20 excellent photos of high standard, facilitating easy comprehension of the text.

Well-selected and abundant references are given at the end of all the studies. A subject index supplements the text.

The book is written in a lucid, simple style and it is easy to understand.

It's typographical layout is also to be praised. It is highly recommended to research workers as well as to students.

Z. TUBA

KEDVES M.: Introduction to the Palynology of Pre-Quaternary deposits.

Studia Biologica Hungarica 19. Part I. pp. 1-164. — 20. Part. II. pp. 1-144.

Akadémiai Kiadó (Publishing House of the Hungarian Academy of Sciences), Budapest.

The increase of the palynological literature makes nearly impossible to give a comprehensive review indicated in the title. There are different catalogues, bibliographies, they make every effort to register the palynological literature. However, chiefly for a beginner it seems impossible to find a way between the different procedures and the massive literature. This book is very helpful in this case. The author of this book has been working in the field of palynology for more than twenty years, on very different subjects.

The first volume reports on general knowledge and methodological procedures. It is desirable to do the review chapter by chapter, because they have many important aspects.

I. Introduction. The author writes on the importance of palynology and the ramifying application of it. It is divided into two parts: fundamental and applied palynology.

II. Chemistry of the spore-pollen wall. A short summary of the constituents and structure of the spore and pollen wall. The author gives his own results as well.

III. Degradation and corrosion. A short summary of the literature.

IV. Preservation. It is connected with the degradation and corrosion.

V. Fluorescence microscopy. In this chapter VAN GIJZEL's (1967) research work is summarized.

VI. Sporoderm stratification. The different views about the morphological nomenclature are presented.

VII. Development of the exine.

VIII. Evolutionary significance of the exine. A summary of the symposium "The evolutionary significance of the exine" held in London (DAHL 1976).

IX. Sporoderm ornamentation.

X. Transmission electron microscopy of recent sporomorphs. The author's names and data are given to the list of the plant they were elaborated with TEM in systematical order.

XI. Scanning electron microscopy of recent sporomorphs. As in the preceding chapter, a list is given.

XII. Morphology of spores and pollen grains. There is a summary of knowledge on the fundamental morphology (Spores, gymnosperm pollen grains,

and angiosperm pollen grains). It is written about the evolution of Dicotyledonopsida pollen.

XIII. Pollen and classification. This chapter informs us about the connection of morphology and systematics.

XIV. Variability, polymorphism. The pollen connected with polymorphism, and the changes due to preparation are illustrated with examples.

XV. Ontogeny of fossil pollen grains. This question is illustrated with important data.

XVI. Transmission electron microscopic study of fossil sporomorphs.

The author has many results in this field. It is a summary of the TEM research from the Precambrian till the Tertiary. At the end of the volume there are 10 plates with TEM photographs by the author.

XVII. Scanning electron microscopic study of fossil sporomorphs.

A list of the authors in order of the geological time table. At the end of the volume, there are 10 plates with SEM micrographs by the author.

XVIII. Associated sporomorphs. It discusses the importance of in situ sporomorphs.

XIX. Questions of nomenclature of fossil sporomorphs. The most important conceptional changes in the nomenclature are dealt with.

XX. Technique. One of the very important questions in the palynology. Different procedures, with the author's own experiences are discussed. The technique of the transmission electron microscopy and the carbon replica method and scanning electron microscopy methods are also given.

XXI. Computers in palynology. It is chiefly written about the necessity of Kremp Paleo Data Banks.

XXII. Books, monographs on the palynology of living plants.

A subject index closed the volume.

As the first volume is useful for all palynologists the second one could be interesting more for the paleo-palynologist. The chapters included are:

I. General problems of investigating fossils. Here are given the general evaluation methods, geological time table.

II. Precambrian-Algonkian. The direction of the research, the principal results and the difficulties are discussed.

III. Cambrian. Chiefly Soviet scientist made fundamental work in this part of palynology.

IV. Silurian. The importance of this period is the appearance of the Cormophyta. After CRAMER (1970c) he presents 5 facies of microfossils and a palynostratigraphical model (CRAMER 1971). He presents a table after RICHARDSON 1974: palynostratigraphy of the Silurian and Devonian and the spore assemblages of the Northern Hemisphere.

The research work of the Ordovician was carried out by Soviet palynologist.

V. Devonian. The knowledge of the Devonian palynostratigraphy is given by RICHARDSON et al. 1964 and CHALONER 1967. A redrawing from CRAMER and DIAZ 1975 is given from the spores characteristic of the Lower Devonian.

VI. Carboniferous. In abbreviated form are given the most important results, with some interesting illustrations, paleophytogeographic regions, succession and main types of sporomorphs of the Carboniferous vegetation.

VII. Permian. The Permian is divided into two parts. The lower part is influenced by the Carboniferous floristic elements, the upper part is characterized by the first flourish of Gymnospermatophyta. The drawings following REINHARDT (1964) present the major short-range sporomorphs from the Carboniferous up to the Triassic. The Late Permian paleogeography, phytogeography of the Sakmarian and a sketch of the Lower Gondwana palynological assemblages complete the chapter.

VIII. Triassic. The author gives an enumeration of the most important achievements of the students of the Triassic. This period witnessed a new flourishing of Gymnospermatophyta. The divergencies in the vegetation between Permian and Triassic resulted from changes in environment.

IX. Jurassic. About the results of the Palynological data of Jurassic, reference is made to ROGALSKA's (1976) table of the Lias and Dogger stratigraphy. A redrawing of the zonation of the vegetation is given.

X. Cretaceous. It is a very important epoch for the evolution of the recent flora. There is a redrawing of the distribution of Dicluripollis etruscus, and a characterization of Lower Cretaceous. The Lower Cretaceous paleophytogeographic provinces of HERNGREEN (1980) are discussed. A separate part is concerned with the appearance of the early angiospermous pollen grains and the evolution of Angiospermatophyta pollen grains and the distribution of ancient angiospermous pollen grains in pre-Aptian, Aptian and Albian time. The Late Senonian and Paleogene phytogeographic map is given.

XI. Tertiary. At first the debate about Cretaceous: Tertiary boundary is discussed.

1. Paleogene. 1.1 Paleocene. Problems of Danian-Paleocene are discussed. The supernove theory is also mentioned. The authors dealing with the Paleocene-point to the differences of the distinct developed formations. The Danian holotype, investigated by KEDVES in 1979, is characterized by Upper Cretaceous Normapollis and Lower Tertiary Postnormapollis. It must be stressed that some of the Angiosperm genera appeared in this period. There are reported the pollen stratigraphy of the Mesozoic and Cainozoic sediments of Southern Sakhalin after ZAKLINSKAIA 1976, and Cretaceous-Paleogene floristic areas and provinces following ZAKLINSKAIA 1966, and Paleocene to Early Eocene paleofloristic provinces in Eurasia following BOITZOVA and PANOVA 1973.

1.2 Eocene. For the vast number of the Eocene palynological literature, the most important ones are reported, including all substages with climatological conclusions. The zonation of the vegetation from the Middle Eocene browncoal sequences of the Dorog basin are reproduced (KEDVES 1960) and the stratigraphy of the Paleocene and Eocene sporomorphs assemblages of the Gulf Coast (USA) and Central Europe, and a map of paleofloristic of Eurasia's Middle and Upper Eocene are given.

1.3 Oligocene. First, the question of the Eocene-Oligocene boundary is discussed. The author introduces important results concerning the Lower-Middle and Upper Oligocene. He refers to the fact, that the paleofloras considerably differ by latitude. He reports on the palynostratigraphy of Upper Tertiary of Turkey and a paleofloristic map of the Oligocene in Eurasia.

2. Neogene. The research work shows a great floristical change in the Upper Oligocene when the vegetation was subtropical.

2.1 Miocene. The palynological results are presented for the Lower-, Middle-, and Upper Miocene. From the Lower Miocene two redrawings are given, the zonation of the swamp responsible for the formation of the lignitebearing sequences and their succession in Hungary.

2.2 Pliocene. From the Lower Pliocene till the Plio-Pleistocene boundary are given the data of the palynological literature.

Finally, at the end of this volume there is a subject index, too. Palynostratigraphical tables are supplemented. The useful handbook is a guide of the palynological work. Each chapter is completed with the list of relevant literature.

E. RODRIGUEZ — P.L. HEALEY — I. METHA (eds): *Biology and Chemistry of Plant Trichomes*. Plenum Press, New York 1984, 255 pp.

For centuries it has been recongized that plants elaborate trichomes (hairs) that produce natural chemicals useful to the plant and man. These trichomes consist of one or more cells which are derived from single proto-dermal cells and have a variety of functions. They refer phytophagous insects and function as protection from excess temperature drop or water loss by covering the plant surface with a trapped air space. Glandular trichomes synthesize, metabolize or accumulate and secrete terpenoids, phenolics, mucroproteins, and resins. Stinging hairs of nettles and other plants not only deter herbivory but in many cases elicit severe cases of skin dermatitis.

Although a number of reviews have been published in the last decades, few have attempted to cover the biology and chemistry of plant trichomes. Therefore, a symposium was organized to bring together scientists working on diverse aspects of plant trichomes. The symposium was hold as a joint meeting of the Botanical Society of America and the Canadian Botanical Society, in Vancouver, Canada on July 11–16, 1980. This volume contains the whole material of the symposium, eight proceedings.

In the first paper, H.D. BEHNKE gives an overall characterization of the structure and ultrastructure of plant trichomes. A general terminology is proposed along with taxonomical applications, and a special trichome — bacteria interaction in leaf tips of *Dioscorea* sp. is given.

P.G. MAHLBERG, Ch.T. HAMMOND, J.C. TURNER and J.K. HEMPHILL deal with the structure, development and composition of glandular trichomes of *Cannabis sativa* L. Based on morphological and physiological differences, they distinguish several types of glandular and non-glandular trichomes in this species, and also their cannabinoid production. Ultrastructural studies have provided an indication of plastid involvement in cannabinoid synthesis.

The systematic implications of flavonoids secreted by certain plant species are discussed by E. WOLLENWEBER. Flavonoid glycosides are very widely distributed in plants. Free flavonoid aglycones have been known to occur externally on leaves and inflorescences of *Primula* and on fronds of *Pityrogramma* species as a farinose deposit, secreted by capitate glandular trichomes. Flavonoids, secreted by a secretory epithelium or by glandular trichomes have been also found in the bud excretions of *Populus*, *Aesculus* and some *Betulaceae* species, and also in several other genera of herbaceous plants, mostly living in semi-arid habitats.

R.L. PETERSON and J. VERMEER discusses the recently available histochemical techniques for determination and identification a wide variety of polysaccharides, proteins, lipins, essential oils, resins and flavonoids secreted by plant trichomes. Most of these techniques have been employed at the light microscope level, but there is a growing number of histochemical techniques adapted to ultrastructural studies of localization of synthesis' site and storage.

For ecophysiologists, this volume presents a very attracting topic. J. EHLERINGER deals with the ecophysiological effects of leaf trichomes on surface spectral characteristics of some desert plants in Utah. Dense trichome layers substantially increase leaf reflectance for all wavelengths of solar radiation between 400 — 3000 nm. Leaf absorptance to total incident solar radiation may be decreased by a factor of three when compared to the leaf absorptance of glabrous leaves. This has a strong effect on leaf temperature, photosynthetic rate and transpiration rate, but

contrary to the general belief, only a little effect on the total leaf resistance to water loss.

Biosynthesis of terpenoids is reviewed by R. CROTEAU and M.A. JOHNSON with particular reference to the mono-, sesqui- and diterpenes, their turnover rates, physiological importance and possible ecophysiological role.

In the last chapter, R.G. KELSEY, G.W. REYNOLDS and E. RODRIGUEZ present a review of biologically active constituents in plant glandular trichomes. These secondary metabolites have been shown to be associated with anti-tumor, cytotoxic, anti-microbial, antifungal, insect-repellent, phytotoxic, growth-regulatory and many other activities. They are also known to poison livestock or to cause allergic contact dermatitis in humans. The authors support the idea that trichomes are really the "first line" of defense of plants against insects and pathogens, and also against herbivores.

As for the whole book, we can say time and again, it is carefully prepared, well-documented and illustrated especially by the magnificent ultrastructural microphotos. It also contains a subject index and a list of participants of the Conference.

We can highly recommend it to every ecophysiologists and phytochemists, it is also a valuable source for plant physiologists and all those who are interested in biologically active constituents in plants, as well as biochemists and cell biologists.

Z. SZŐCS

Donald B. RODDYN (ed.): Subcellular Biochemistry. Volume 9. Plenum Press. New York and London 1983, pp. 425.

This long-needed book has been written for everybody who wants to get a deeper insight into electron microscopic methods in biology, principles and problems of chloroplast protein synthesis, a novel kind of nucleoprotein particle, platelet phospholipid as symmetry and the diversity of function and structure of cellular membranes. The present book is the 9th volume of an ongoing series of high standard.

The present volume consists of five main chapters. Each chapter comprises different subchapters, facilitating easy comprehension of the text.

Chapter 1 includes an extensive account of electron microscopy. It consists of 7 subchapters. The introduction is followed by the discussion of the electron microscope, including the signal formation and special imaging techniques in transmission electron microscopes. Furthermore, this subchapter also deals with surface imaging and image recording.

The next two parts of this chapter discuss preparation and analysis-functional aspects. We can get acquainted with the physical background of numerous methods, such as chemical, physical methods, with groups- and charge specific "stains" and enzymatic digestion, enzyme cytochemistry, marker molecules, immunocytochemistry, lecitin labelling, autoradiography, morphometry, X-ray microanalysis, ion precipitation.

There is a particularly useful and important section: "Molecular Electron Microscopy", including techniques for the study of nucleic acids. We can also read a brief summary of units and conventions, and perspectives at the end of the chapter.

The paper is well supplied with tables, diagrams and sample electron micrographs.

The next chapter deals with the problems and principles of chloroplast protein synthesis. In the second section of this chapter, the author presents basic concepts of governing nuclear-chloroplasts. The five principles are as follows: 1) most chloroplastal proteins are encoded by molecular genes and made on cytoplasmic ribosomes, 2) these proteins enter the chloroplast by a posttranslation process in the envelope, 3) the chloroplast genome is essential and codes for about 100 polypeptides, 4) proteins and RNA coded by the chloroplastal genome function only within the chloroplast, 5) light stimulates the accumulation of chloroplastal proteins.

In the further parts of the chapter the nucleocytoplasmic origin of the chloroplast polypeptides, the essential contribution of the chloroplast genome, the confinement of chloroplast DNA-encoded molecules and the stimulatory role of light are discussed in detail.

Chapter 3 is entitled "Thesaurisomes, a novel kind of nucleoprotein particle". The meaning of the Greek word of thesaurisomes: thesauros (treasure), soma (body). The particles discussed here are interesting; they may well constitute an important new class of ribonucleoprotein complexes of general biological significance. The biochemical characteristics of these particles and the relationship between thesaurisomes and ribosomes are described in detail.

The next article gives an account of the asymmetry of phospholipids in platelets and the significance of platelet hemostatic activities.

First, the authors survey the general properties of nonactivated and activated platelets, then they discuss the asymmetry of membrane lipid in erythrocytes and platelets.

In the following section of the chapter, the authors deal with the relationship between phospholipid orientation and the hemostatic activity of platelets.

The greatest value of this study is the clear description of the clinical importance and the biochemical model system of biomembranes.

The final chapter discusses the diversity function and structure of cellular membranes, such as membrane of mitochondria, photoreceptors and plasmamembrane. There are excellent micrographs supporting the author's theories.

Finally, as an unusual but interesting part, an extensive and detailed book review is found in the volume. The topics of books discussed are the following:

- 1) Evolution and Development;
- 2) Plant Cell Biochemistry;
- 3) Miscellaneous topics.

The general presentation of the book is of a high standard, the subject is presented in a readable and stimulating style.

No separate bibliography is provided, dozens of references are listed at the end of each chapter. The whole volume is well-illustrated and an index is also supplied.

It should not be absent from libraries and is recommended for individuals interested in new results of subcellular biochemistry.

Z. TUBA

J. SCHULTZE-MOTEL (ed.): Rudolf MANSFELD'S Verzeichnis Landwirtschaftlicher und Gartnerischer Kulturpflanzen, Akademie Verlag, Berlin. 1986. 4 volumes, 1998 pages, 241 illustrations.

This book, which is unique by any standard, is the continuation of Prof. Rudolf MANSFELD's "Vorläufiges Verzeichnis landwirtschaftlich oder gärtnerisch kultivierter Pflanzenarten (mit Ausschluss von Zierpflanzen)"—*Prodromus enumerationis specierum plantarum agri et horticulurae (Plantis ornamentalibus exceptis)*, published in 1959, a year before the author's death.

Whereas in the first edition a total of 1430 plant species was enumerated, in this extended and completely revised book about 4800 cultivated plants of species rank are discussed. Additional taxa are the species used in cultivation experiments and plant breeding and the wild species potentially cultivated etc. The review of the relevant literature of the past 20 years contributed to the increase of species number in each category of utilization and also to the introduction of new categories.

The species discussed belong to 230 families, follow ENGLER's "Syllabus der Pflanzenfamilien" (1954, 1964).

The two economically most important families are the Leguminosae and Graminae, represented by 658 and 600 species, respectively. Over 100 species are included in the book from the following families: Rosaceae (226), Compositae (215), Euphorbiaceae (136), Labiatae (127), and Solanaceae (115). The number of species is between 50 and 100 for the Liliaceae (88), Agavaceae (78), Moraceae (73), Myrtaceae (71), Palmae (82), Rutaceae (78), Umbelliferae (75), Zingiberaceae (64), Polygonaceae (57), and Rubiaceae (51). More than half of the 230 families are represented by less than 10 species, and only one cultivated species is mentioned from 45 families.

The systematic discussion is detailed to the subspecies level; lower ranks are treated only in exceptional cases. The following data characterize each species: name, taxonomic data and synonyms, popular name(s), distributional data, area of cultivation, utilization, in some cases notes on the phylogeny of the plant, discussion of its variability, history of its use, closest relatives as ancestors of the cultivated taxon, and references.

In the introductory notes reference is made to the difficulties with cultivated plants. There are problems still existing just as 25 years ago, when the first edition was published. These are, for example: in some groups (Arachis, Solanum, Malus, Pyrus, etc.) the taxonomic knowledge is insufficient, the species concept is not uniformly used, and the taxonomic structures are too complicated (e.g., Medicago, Triticum, Citrus). In some cases nomenclatural problems are unsolved. The list of cultivated plants of China or Central Africa is still incomplete; and it is often unclear whether an utilized plant is cultivated or not. The authors call the attention of the reader on recently published reports on these plants.

In Volume 1 (577 pages), 96 families are discussed and 79 illustrations supplement the text. The taxa discussed are Schizophyta (2 species), Phycophyta (11 families, 23 species), Fungi (13 families, 31 species), Pteridophyta (5 families, 11 species), and Gymnospermae (7 families, 20 species). Fifty-eight families of dicotyledonous species, numbering 1400, are listed.

Volume 2 (548 pages, 73 illustrations) continues with the Leguminosae: Major genera are Trifolium (35 species), Medicago (21), Vicia (23), and Lathyrus (18). Some additional major families in the volume, re-

presenting these 81 families are: Euphorbiaceae (136 species), Umbelliferae (75 species), Anacardiaceae (57 species), Cucurbitaceae (52 species), Rubiaceae (51 species), Apocynaceae (48 species) etc.

Volume 3 (519 pages, 86 illustrations) includes 45 families from Labiatae to the Orchidaceae. Thirty of them are monocotyledonous. The number of cultivated species in the 15 dicotyledonous families is about 570. Most species are from the Compositae family (over 200), and the Labiatae and Solanaceae are also represented by many species.

The 30 families of Monocotyledoneae are represented by 1160 cultivated species. Of course, the Gramineae family has the highest number of species. Triticum has 28 cultivated species, Avena has 16, Secale has 9, Panicum has 18, and Sorghum has 9.

Volume 4 has 301 pages. Its first chapter reviews the families of cultivated plants (230 families altogether). Then, the list of new combinations follows, containing 39 new combinations, amendments, new nomenclatural and taxonomic assignments for 13 families.

The chapter "Literature" presents 4600 items on 168 pages plus 312 additional citations as a supplement. There is a 20-page supplement to the text (Nachträge zum Text), containing 370 species (Gramineae 37, Leguminosae 21, Polygonaceae 15, Euphorbiaceae 14, Myrtaceae 16 species, etc.).

The genera and species are classified according to their utilization in the "Register" (Übersicht der Arten nach dem Kulturzweck). This helps the reader find particular plant species in utilization categories. The 50 categories are as follows: Plants containing volatile oils (41 families, 138 species), flavouring plants (Aromatisieren von Speisen, Getränken, 11 families, 13 species), melliferous plants (Bienenfutter, 15 families, 47 species), soil covers (Bodenbedecker, 18 families, 94 species), soil hardeners (Dünenbefestigung, Sandbefestigung, Erosionsschutz siehe auch Rekultivierung, 56 families, 303 species), dye plants (41 families, 76 species), fiber plants (28 families, 97 species), fish and bird food (3 families, 7 species), fish poison (13 families, 25 species), spinning material (Flechtmaterial, siehe auch Faserpflanzen, 13 families, 40 species), fodder plants (Futterpflanzen, Weidepflanzen, 40 families, 345 species of which 101 belong to the Leguminosae, 115 to the Gramineae), vegetables (siehe auch Knollenpflanzen und Speisepilze, 94 families, 445 species), drugs and refreshing materials (Genussmittel, Anregungsmittel, siehe auch Halluzinogene, 13 families, 18 species), tanning materials (17 families, 34 species), drinks (Getränke ausser Genussmittel, 29 families, 69 species), cereals (Gramineae, 37 species), spices (42 families, 152 species), green fertilizers (Gründungspflanzen, Bodenverbesserung, Stickstoffanreicherung, 16 families, 132 species), narcotics (Halluzinogene, psychotrope, Drogen, Rauschmittel siehe auch Genussmittel, 9 families, 18 species), resiniferous plants (Harze, 10 families, 19 species), hedgerow plants (Heckenpflanze siehe auch Windschutzpflanzen, 65 families, 303 species), medicinal plants (Heilpflanzen, Arzneipflanzen, Drogen, Medizinalpflanzen, 138 families, 725 species or genera), insecticides (12 families, 26 species or genera), rubber plants (Guttapercha, Gummi, Latex, 12 families, 45 species), tuber crops (Knollenpflanze, 25 families, 68 species or genera), nuts, edible seeds (Nüsse, 71 families, 231 species or genera), fruits (53 families, 185 species or genera), oil plants (Ölpflanzen, 35 families, 80 species or genera), paper-plants (11 families, 17 species or genera), arrow poison (7 families, 16 species or genera), pseudocereals (3 families, 7 species or genera), lawn plants (5 families, 27 species or genera), plants used for recultivation (13 families, 32 species or genera), saponine plants (5 families, 11 species or genera), shade plants (36 families, 126 species), jewel plants (4 families, 4 species), plants protecting against animals (5 families, 7 species), silkworm food (8 families, 14 species), soda and salt

plants (6 families, 9 species), starch plants (2 families, 6 species), edible mushrooms (1 family, 16 species), supporting plants (11 families, 15 species), relaxing plants (3 families, 4 species), miscellaneous materials (33 families, 54 species), wax and lipid plants (Wachse und technische Fette, 7 families, 11 species), plants protecting against wind (39 families, 106 species), host plants for cochineals (1 family, 6 species), host plants for shellac producing insects (7 families, 14 species), "magic" plants (Zauberpflanzen, 33 families, 70 species), sugars and other sweetening materials (7 families, 9 species).

To exemplify the manifold usefulness of the "register", we show what kind of information may be obtained regarding the Solanaceae family. The cultivated species of this family may be found in 18 utilization categories: soil hardeners (Cestrum parquii), soil covers (Salpichroa), dye plants (Capsicum annum, Cyphomandra hartwegii), fodder plants (Nicandra), vegetables (Lycium chinense, Physalis longifolia, Solanum lycopersicum, Capsicum, Cyphomandra), drugs (Nicotiana), spices (Physalis philadelphica, Solanum erianthum, S. anomalum, S. dasyphyllum, S. macrocarpon, S. aethiopicum, S. anguivii, S. distichum, Capsicum), narcotics (Ichroma fuchsoides, Datura, Brunfelsia hopeana, Justicia pectoralis), hedgerow plants (Lycium, Solanum sisymbriifolium, S. aculeastrum, Cestrum), medicinal plants (Nicandra, Atropa, Scopolia, Physoclaina, Hyoscyamus, Withania, Physalis alkekengi, Ph. minima, Jaltomata, Solanum aviculare, S. laciniatum, S. marginatum, S. xanthocarpum, S. viarum, S. mammosum, S. dulcamara, Capsicum annum, Datura, Cestrum nocturnum, C. pseudoquina, Fabiana, Nicotiana glauca, A. attenuata, Duboisia, Brunfelsia), insecticides (Nicotiana glauca), tuber crops (Solanum), edible seeds (Lycium pallidum, Physalis viscosa, Solanum, Mandragora), fruits (Ichroma australe, Physalis peruviana, Ph. pruinosa, Solanum muricatum, S. laximitante, S. quitoense, S. stramonifolium), shade plants (Solanum giganteum), miscellaneous (Nicotiana rustica), plants protecting against wind (Cestrum laevigatum), magic plants (Solanum triflorum, S. amictum).

The "Register" is followed by the list of popular names on 47 pages. Then, the list of botanical names is presented on 48 pages. Errata corrigenda close the volume.

The plants, as renewable sources of energy, play an obvious role to solve the nutritional and industrial problems in the world, and their importance will be even higher in the future. This fact gives timeliness to this unique synthesis of cultivated plants.

This work is an indispensable source of information for anyone dealing with cultivation, plant breeding and industrial utilization of plants and for other experts and amateur botanists.

I. MÁTHÉ sen.

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STATE OF PALYNOLOGICAL RESEARCH IN HUNGARY

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The first works on palynology in Hungary appeared in the past century. JURÁNYI's pioneer professional activity (1870-1884) was important not only from a Hungarian point of view; his results concerning the ontogeny of pollen grains in the genus Ceratozamia were referred to even in recently published foreign papers (cf. AUDRAN, 1970). The first Hungarian work on pollen morphology was written by BALÁZS (1896) who after giving a basic knowledge described the pollen grains of 64 angiospermous families.

The spore-pollen research entered its second phase in the first half of this century when, after a long pause investigations started in various lines. Results of interesting studies of biological character were published by GREGUSS (1926, 1927, 1928, 1929a, b). The exploration of Quaternary fens began in Hungary on the initiation of SOÓ (1926). The results attained by ZÓLYOMI (1931, 1936, 1937, 1952) concerning forest- and climate development in the post-Pleistocene raised the Quaternary palynology of Hungary to an international level. In 1932, from the carbonaceous Eocene layers of Dorog GELLETICH made the first spore-pollen analyses under the guidance of POTONIÉ. The first pollen data from the Hungarian Pliocene appeared in 1937 after ZÓLYOMI's investigations (FRANZ, HÖFLER and SCHERF). GREGUSS (1940) published the results of pollen analyses of mammoth- and carbon finds at Szeged-Üthalom, then wrote the monograph of spores of Central European pteridophytes (1941). HAZSLINSZKY jr. (1938, 1943, 1952, 1955) laid the foundations of the melittopalynological research in Hungary.

Since the fifties the Hungarian palynological investigations have been carried on in various fields with an extremely high intensity. Although the development is uneven, the research fields are arranged in a system:

1. ACTUOPALYNOLOGY

1.1. Spore- and pollen morphology

Results of recent studies completing the investigations of pre-Quaternary palynology were published in the first place. Thus, with the spores of Pteridophytes the ontogenetic and taxonomic questions of trilete - triplane and poroplane variations were discussed by DEÁK (1959a) and KEDVES (1960, 1961a). Latter published data of such character on the intraspecific variation of pollen grains from GINKGO (1961b) and some Angiospermatophytes (1979) too. Comparative morphological examinations were carried out by JÁRAI-KOMLÓDI (1974) with spores of Funaria and Physcomitrium, and by JÁRAI-KOMLÓDI and ORBÁN (1975) with those of European Encalypta species.

1.2. Palynotaxonomy

Works on taxonomy of Rondeletieae (Rubiaceae) were published by BORHIDI, JÁRAI-KOMLÓDI and MONCADA (1980), BORHIDI (1982), BORHIDI and JÁRAI-KOMLÓDI (1983), BORHIDI and FERNANDEZ ZEQUEIRA (1981a, b; 1983). Monographic work is the book of BOROS and JÁRAI-KOMLÓDI (1975): "An atlas of recent European moss species." The material treated in KEDVES' work on pollen grains of Palmae (1980) is of larger volume.

1.3. Out of the publications of methodological character works by FISCHER and JÁRAI-KOMLÓDI (1970), ROWLEY and JÁRAI-KOMLÓDI (1976), JÁRAI-KOMLÓDI (1980) and ZÓLYOMI and PRÉCSÉNYI (1985) should be mentioned.

1.4. Aeropalynology

The number of children and grown-ups suffering from pollen allergy is increasing year by year. However, this branch of palynology, though highly important if only from a medical point of view, has not unfortunately developed to a desirable extent in Hungary. Results of initial examinations were published by SIMONCSICS, OSVÁTH and BALÁZS (1970), and OSVÁTH, BALÁZS and SIMONCSICS (1970).

1.5. Ampelological palynology

Valuable data on the pollen grains of Hungarian grape-vine varieties were supplied in the last several years by the scanning electron microscope examinations (TOMPA-KASHIRSKAYA and KOZMA, 1978, 1981).

1.6. Agronomical palynology

From a practical point of view particularly important are the investigations related with the viability, lifetime and tolerance to environmental effects of cereal pollens.

Results of preserving Zea mays pollen grains were published by BARNABÁS and RAJKI (1981) and BARNABÁS and FRIDVALSZKY (1984). They found that after losing 65–75 per cent of the original water content through drying the pollen grains could still be rehydrated and the pollen tube developed. Using a new staining method PÁLFI G. and PÁLFI ZS. (1982), PÁLFI G. and KÖVES (1984) and PÁLFI G. and GULYÁS (1985) found a positive correlation between the prolin content of pollen grains and the formation and fertility of the pollen tube. SZABÓ, GULYÁS and FRANK (1984) described the differences between sterile and fertile pollen grains of Helianthus annuus.

2. PALAEOPALYNOLOGY

A hand-book by KEDVES (1986a, b): Introduction to the Palynology of pre-Quaternary deposits, 1–2.

2.1. Examination of associated sporomorphs

On Hungarian macrofossils only two data have been published so far (ANDREÁNSZKY, 1949; KEDVES, 1965).

2.2. Examination of disperse sporomorphs

Since the beginning of the fifties wide investigations have been carried on in this scope of subject.

Palaeozoic

It is less known as yet; on the Silurian (GÓCZÁN, 1971a) and Carboniferous (GÓCZÁN, 1971b) preliminary studies have been published. On the Permian much more palynological data are available (DEÁK, 1959b; STUHL, 1962).

Mesozoic

Iriassic — On the basis of publications by VENKATACHALA and GÓCZÁN (1964) and BÓNA (1972, 1979, 1984) it is relatively well known.

Jurassic — A detailed palynological processing of sporomorphs from the coal beds of Komló (GÓCZÁN, 1956; BÓNA, 1963, 1966, 1969) on the one hand,

and of the manganese ore of Úrkút (SIMONCSICS and KEDVES, 1961; KEDVES and SIMONCSICS, 1964) on the other hand was accomplished.

Cretaceous — The foundations of a palynological knowledge were laid down by DEÁK (1961, 1962, 1963, 1964, 1965) for the Lower-Cretaceous and by GÓCZÁN (1964, 1967, cf. GÓCZÁN, GROOT, KRUTZSCH and PACLTOVÁ) for the Upper-Cretaceous of Hungary. The taxonomic processing of monosulcat pollens from the Albian stage was carried out by GÓCZÁN and JUHÁSZ (1984, 1985). Results of exploration were recently published by RÁKOSI (1970) and JUHÁSZ (1972, 1975, 1979, 1980, 1983) for the Lower- and by KEDVES and DINIZ (1983), KEDVES (1984, 1985) and SIEGL-FARKAS (1983, 1984, 1985) for the Upper-Cretaceous.

Cainozoic

Palaeogene

The Eocene of Hungary is well known from the works of KEDVES (1960, 1961a, 1965, 1969, 1973, 1974, 1978, 1986c), KRIVÁN-HUTTER (1961), RÁKOSI (1966, 1968, 1971, 1973, 1977, 1978, 1979, 1983) and RÁKOSI and TÓTH (1980). Somewhat less known though properly treated is the Oligocene (RÁKOSI, 1980) and the Egerian, the transitional Paratethys stage of Oligocene-Miocene (E. NAGY 1963b, 1979a).

Neogene

On the basis of investigations by MAÁ CZ and SIMONCSICS (1956), E. NAGY (1957, 1958, 1959, 1960, 1962, 1963a, c, 1965, 1966, 1967, 1968, 1969, 1973, 1976a, b, 1979b, 1980, 1982, 1985), SIMONCSICS (1959, 1960, 1963, 1969), NAGY-BODOR (1982) and SÜTŐ-SZENTAI (1983) this epoch is also well known.

Plio-Pleistocene and Pleistocene

Results of peat-bog examinations were published by SZALAY (1943). Exploration in the Great Hungarian Plain as a task of priority is in process (CSINÁDY, 1953, 1954; VOZÁRY, 1957; MIHÁLTZ-FARAGÓ, 1966, 1976, 1979, 1982; MIHÁLTZ-FARAGÓ and MUCSI, 1971; JÁRAI-KOMLÓDI, 1965, 1966, 1968, 1973; NAGY-BODOR, 1983). The history of the development of Lake Balaton is known from the investigations of ZÓLYOMI (1952). Information on plant remains in recent lake deposits and on the results of chemical analysis of mud was given by KEDVES and KÖRMÖCZI (1985).

Results of archeological implication are relatively scarce (ZÓLYOMI and PRÉCSÉNYI, 1985).

3. SPORODERM ULTRASTRUCTURE EXAMINATIONS

First of all fossil angiospermous pollen grains were subjected to this examination (e.g. KEDVES and PÁRDUTZ, 1970, 1983; KEDVES, 1981).

4. Results of the first experiments related with the molecular structure of the sporopollenine biopolymer were published in the near past (KEDVES, 1986c, d, e).

Summing up the past and the present state of palynological research in Hungary we can say that in spite of the difficulties we have succeeded in showing up results that even catch the attention of the international professional circles. We have reached the international level in the application of up-to-date methods as well. Furthermore, Hungarian palynologists have taken part in realizing several international research programmes. On the other hand, the disproportion of the different research fields is remarkable, the deficiencies, in particular, are regrettable, e.g. the neglect of Melittopalynology, or of studies with medical implications just started.

The importance of palynological research in everyday life does not call for evidence, and the increasing demands themselves will result in a new upswing in these investigations.

REFERENCES

- Andreánszky, G. (1949): Reste einer neuen tertiären Palme aus Ungarn. Hung. Acta Biol. 1: 31-36.
- Audran, J.-C. (1970): Sur l'ultrastructure de la paroi pollinique chez le Ceratozamia mexicana (Cycadacées). Pollen et Spores 12: 485-511.
- Baláss, I. (1890): A pollenről különös tekintettel a honi Angiospermae fajokra. (About pollen grain with special interests to Angiosperm species). In Hungarian. Kolozsvár, 91. o.
- Barnabás, B., Fridvalszky, L. (1984): Adhesion and germination of differently treated maize pollen grains on the stigma. Acta Bot. Hung. 30: 329-332.
- Barnabás, B., Rajki, E. (1981): Fertility of deep-frozen maize (Zea mays L.) pollen. Ann. Bot. 48: 861-864.
- Bóna, J. (1963): A mecseki liász feketekőszéntelepek távazonosítására irányuló palynológiai vizsgálatok. (Palynological studies for remote identification of carboniferous deposits of lias in Mecsek). In Hungarian. Földt. Közl. 93: 15-23.

- Bóna, J. (1966): Spores de Lycopodiaceés dans le charbon Liasique du Mecsek. Acta Bot. Acad. Sci. Hung. 12: 27–32.
- Bóna, J. (1969): A Mecsek hegység alsóliász kőszénösszlete. (The carbon coal deposits of lower lias in Mecsek Mountains). In Hungarian. Palynologia. Ann. Inst. Geol. Publ. Hung. 51: 625–671.
- Bóna, J. (1972): A mecseki alsóliász és felsőtriász rétegek palynológiai vizsgálata. (Palynological studies of the lower lias and upper triassic layers in Mecsek). In Hungarian. Thesis Cand. Sci. 1–14.
- Bóna, J. (1979): A Máza-Dél-Váralja-Dél feketekőszénösszlet pollenvizsgálati eredményei. (Results of palynological studies carried out on coal deposits of Máza-South-Váralja-South). In Hungarian. Földtani Kutatás 26: 70–80.
- Bóna, J. (1984): Szintjelző spórák és virágporaszemek a Kelet-Mecseki felsőtriász kőszénfekű rétegekből. (Stratus-indicator spores and pollen grains from the Upper-triassic carboniferous strata of the East-Mecsek Mountains.) In Hungarian. Folia Comloensis 1: 3–25.
- Borhidi, A. (1982): Studies in Rondeletieae (Rubiaceae) III. The genera Rogiera and Arachnothryx. Acta Bot. Acad. Sci. Hung. 28: 65–71.
- Borhidi, A., Fernandez Zequeira, M. (1981a): Studies in Rondeletieae (Rubiaceae), I. A new genus: Roigella. Acta Bot. Acad. Sci. Hung. 27: 309–312.
- Borhidi, A., Fernandez Zequeira, M. (1981b): Studies in Rondeletieae (Rubiaceae), II. A new genus: Suberanthus. Acta Bot. Acad. Sci. Hung. 27: 313–316.
- Borhidi, A., Fernandez Zequeira, M. (1983): Studies in Rondeletieae (Rubiaceae), V. Los limites del género Suberanthus. Acta Bot. Hung. 29: 29–34.
- Borhidi, A., Járαι-Komlódi, M. (1983): Studies in Rondeletieae (Rubiaceae), IV. A new genus: Javorkaea. Acta Bot. Hung. 28: 13–27.
- Borhidi, A., Járαι-Komlódi, M., Moncada, M. (1980): Acunaeanthus, a new genus of Rubiaceae. Acta Bot. Acad. Sci. Hung. 26: 277–287.
- Boros, Á., Járαι-Komlódi, M. (1985): An atlas of recent European Moss spores. Akadémiai Kiadó, Budapest.
- Csinády, G. (1953): A bátorligeti láp pollenanalitikai vizsgálata. (The palynological study of the Swamp of Bátorliget.) In Hungarian. In Székessy: Bátorliget élővilága. Akadémiai Kiadó, Budapest: 449–453.
- Csinády, G. (1954): A bátorligeti láp története a pollenanalízis tükrében. (The history of the Swamp of Bátorliget with respect to its - palynological study.) In Hungarian. Földr. Ért. 3: 684–690.
- Deák, H.M. (1959a): Observations concernant le changement de forme des spores trilettes. Rev. de Micropaléont. 1: 28–30.
- Deák, H.M. (1959b): A Mecsek-hegységi gipsz kísérleti palinológiai vizsgálata. (Experimental palynological analysis of gypsum deposits on the Mecsek Mountains. In Hungarian. Földt. Közl. 89: 170–173.
- Deák, H.M. (1961): A Bakony-hegység apti képződményeinek és bauxittelepének palynológiai vizsgálata. (Palynological study of the Aptian deposits and bauxit strata of the Bakony-Mountains.) In Hungarian. MÁFI Évkönyve 49: 645–638.

- Deák, H.M. (1962): Két új spóra genusz az apti agyag-márga sorozatból. Földt. Közl. 92: 230-235.
- Deák, H.M. (1963): Quelques spores striées de l'étage Aptien. Rev. de Micro-paléont. 4: 250-256.
- Deák, H.M. (1964): Contribution a l'étude palynologique de groupe d'argiles a Munieria de l'étage Aptien. Acta Bot. Acad. Sci. Hung. 10: 95-126.
- Deák, H.M. (1965): A dunántúli középhegység apti üledékeinek palynológiai vizsgálata. Geol. Hung. Palaeont. 29-32: 9-105.
- Fischer, J., Járαι-Komlódi, M. (1970): Fosszilis keverék pollenek azonosításának matematikai módszere a Picea omorica és Picea abies esetében. Bot. Közlem. 57: 59-68.
- Gelletich, J. (1932): Sporen- und Pollenuntersuchung einer eozänen Braunkohle aus Dorog (Ungarn). Geol. Meldearbeit Techn. Hochschule, Berlin.
- Góczán, F. (1956): Pollenanalytische (palynologische) Untersuchungen zur Identifizierung der liassischen Schwarzkohlenflöze von Komló. MAFI Év-könyve 45: 167-212.
- Góczán, F. (1964): Stratigraphic Palynology of the Hungarian Upper Cretaceous. Acta Geol. 8: 229-264.
- Góczán, F., Groot, J.J., Krutzsch, W., Pacitová, B. (1967): Die Gattungen des "Stemma Normapolles Pflug 1953b" (Angiospermae). Neubeschreibungen und Revision europäischer Formen (Oberkreide bis Eozän). Paläont. Abh. B. 427-633.
- Góczán, F. (1971a): Adatok az alsóörsi, szalatkai és upponyi "szilur" kovalák mikroplankton vizsgálataihoz. (Contributions to the microplankton studies of the fen-states from Uppony, Szalatnak and Alsóörs.) In Hungarian. Öslénytani Viták 18: 13-20.
- Góczán, F. (1971b): Tájékoztató jellegű rétegtani palinológiai vizsgálatok hazai karbon időszaki képződményeken. (Preliminary palynological studies on the sediments of the Hungarian carbon period.) In Hungarian. MAFI évi jelentése az 1969. évről, 677-701.
- Góczán, F., Juhász, M. (1984): Monosulcate pollen grains of Angiosperms from Hungarian Albian sediments, I. Acta Bot. Hung. 30: 283-319.
- Góczán, F., Juhász, M. (1985): Monosulcate pollen grains of Angiosperms from Hungarian Albian sediments, II. Acta Bot. Hung. 31: 69-88.
- Greguss, P. (1926): Die Sporenverwandschaft der Musci. Bot. Archiv. 11: 473-480.
- Greguss, P. (1927): A kétlaki és egylaki növények virágporaszeme. (Pollen grains of monoic and dioic plants.) In Hungarian. Mat. Term. Tud. Közl. 378-394.
- Greguss, P. (1928): A virágporaszemek nagysága és a nemiség meghatározására vonatkozó vizsgálataim. (Studies on the size of the pollen grains and the sexuality of the flowers.) In Hungarian. Debreceni Tisza I. Tud. Társ. II. (orvos-term. tud.) Oszt. Munkái 3: 33-56.
- Greguss, P. (1929a): A Bryonia dioica virágporaszemeinek nagysága és a nemiség meghatározása. (The size of the pollen grains of Bryonia dioica and the determination of its sex.) In Hungarian. Bot. Közlem. 88: 18-22.
- Greguss, P. (1929b): A Melandrium album pollentömlőinek hosszúsága és a nemiség determinációja közötti összefüggés. (Correlation between the

- length of pollen syphon and the sexual character of the flowers in *Melandrium album*.) In Hungarian. Mat. Term. Tud. Értesítő 46: 514–524.
- Greguss, P. (1940): A Szeged-Üthalmi mammut és szénlelet pollenanalitikai vizsgálata. (Palynological study on mammoth rests and the coal deposit of Szeged-Üthalom.) In Hungarian. Szeged Városi Múzeum Kiadványai.
- Greguss, P. (1941): Die Sporen der Mitteleuropäischen Pteridophyten. Mat. és Term. Tud. Közl. 29: 1–25.
- Hazslinszky, B. (1938): Adatok a méz pollenanalitikai vizsgálatához. (Contributions to the palynological study of the honey.) In Hungarian. Mezőgazd. Kut. 11: 143–159.
- Hazslinszky, B. (1943): A nemes gesztenye, mint mézelő növény. (The maroon as honey plant.) In Hungarian. Kertészeti és Szőlészeti Főisk. Közlem. 9: 15–26.
- Hazslinszky, B. (1952): Magyar akácmézek kvalitatív és kvantitatív pollenanalitikai vizsgálata. (Qualitative and quantitative palynological studies on the honey of *Robinia pseudoacacia* in Hungary.) In Hungarian. MTA Biol. Oszt. Közlem. 1: 317–417.
- Hazslinszky, B. (1955): A méz pollenanalitikai vizsgálatának és a pollen-spektrumok kiértékelésének kérdéséhez. (To the evaluation of the pollen spectra and the palynological studies of the honey.) In Hungarian. Élelmiszervizsgálati Közl. 1: 3–18.
- Járai-Komlódi, M. (1965): Palinológiai vizsgálatok a Magyar Alföldön a Würm glaciális és a holocén klíma- és vegetációtörténetére vonatkozóan. (Palynological studies of the Hungarian Plain with respect to the Climate- and Vegetation history during the Würm-glacial and the Holocene.) In Hungarian. Kand. Ért. Tézisei: 1–13.
- Járai-Komlódi, M. (1966): Études palynologiques des couches de la dernière époque glaciaire (Brorup, Pléniglaciaire) de la Grande Plaine Hongroise. Pollen et Spores 8: 479–496.
- Járai-Komlódi, M. (1968): The Late Glacial and Holocene flora of the Hungarian Great Plain. Ann. Univ. Sci. Budapest, Sect. Biol. 9–10: 199–225.
- Járai-Komlódi, M. (1972): Role and importance of Pleistocene and Holocene Palynology. Jb. geol. Bundesanst. 19: 38.
- Járai-Komlódi, M. (1974): Comparative spore morphological examinations in *Funaria* and *Physcomitrium* species. Acta Bot. Acad. Sci. Hung. 20: 71–81.
- Járai-Komlódi, M. (1980): Módszertani tanulmány *Linum* virágporaszemeken fény (LM) és elektronmikroszkóppal (TEM, SEM) történő összehasonlító vizsgálatokhoz. (Methodological study on *Linum* pollens for comparative investigations carried out with light and electron microscope (LM, TEM, SEM.) In Hungarian. Bot. Közlem. 67: 37–47.
- Járai-Komlódi, M., Orbán, S. (1975): Spore morphological studies on recent European *Encalypta* species. Acta Bot. Acad. Sci. Hung. 21: 305–345.
- Juhász, M. (1972): Study of the Trilites formgenus in Lower Cretaceous deposits. Acta Biol. Szeged 18: 43–53.
- Juhász, M. (1975): Lycopodiaceae spores from Lower Cretaceous deposits of Hungary. Acta Biol. Szeged 21: 21–34.
- Juhász, M. (1979): Investigation of some spore genera from the Lower and Middle Cretaceous in Transdanubia. Acta Biol. Szeged 25: 49–64.

- Juhász, M. (1980): Bryophyte spores from Hungarian Early Cretaceous rocks. Acta Biol. Szeged 26: 51-62.
- Juhász, M. (1983): Palynostratigraphic zonation of the Transdanubian Middle Cretaceous. Acta Geol. Hung. 26: 41-68.
- Jurányi, L. (1870): Ueber der Bau and die Entwicklung des Pollen bei Ceratozamia longifolia Miq. Jahrb. Wiss. Bot. 8: 382-400.
- Jurányi, L. (1882): Beiträge zur Kenntnis der Pollen-Entwicklung der Cycadean und Coniferen. Bot. Zeitung 47/48: 1-7.
- Jurányi, L. (1884): Über den Pollen der Gymnospermen. Math. u. Naturwissensch. Ber. 2: 1-17.
- Kedves, M. (1960): Études palynologiques dans le Bassin de Dorog I. Pollen et Spores 2: 89-118.
- Kedves, M. (1961a): Études palynologiques dans le Bassin de Dorog II. Pollen et Spores 3: 101-153.
- Kedves, M. (1961b): Beobachtungen an den Pollen des rezenten Ginkgo biloba L. mit besonderer Hinsicht auf die Fragen der Determination der fossilen Pollen der Ginkgoinae. Acta Biol. Szeged 7: 31-37.
- Kedves, M. (1965): Contributions à la connaissance palynologique de l'Eocène hongrois. Acta Bot. Hung. 11: 325-360.
- Kedves, M. (1969): Palynological Studies on Hungarian Early Tertiary Deposits. Akadémiai Kiadó, Budapest.
- Kedves, M. (1973): Paleogene fossil sporomorphs of the Bakony Mountains Part I. Studia Biol. Acad. Sci. Hung. 12: 1-134.
- Kedves, M. (1974): Paleogene fossil sporomorphs of the Bakony Mountains Part II. Studia Biol. Acad. Sci. Hung. 13: 1-124.
- Kedves, M. (1978): Paleogene fossil sporomorphs of the Bakony Mountains Part III. Studia Biol. Acad. Sci. Hung. 15: 1-166.
- Kedves, M. (1979): Intraspecific morphological variations at recent Angiospermatophyta pollen grains. Acta Biol. Szeged 25: 65-68.
- Kedves, M. (1980): Morphological investigation of recent Palmae pollen grains. Acta Bot. Acad. Sci. Hung. 26: 339-373.
- Kedves, M. (1981): The evolutionary significance of the Angiospermous exine ultrastructure and sculpture. Intern. Symp. Concept. Meth. Paleo. Barcelona 1981: 75-83.
- Kedves, M. (1984): Upper Cretaceous sporomorphs from the southern part of Hungary (Csákvölgy). Acta Biol. Szeged 30: 75-89.
- Kedves, M. (1985): The present day state of Upper Cretaceous palaeophytogeography on palynological evidence. Acta Biol. Szeged 31: 115-127.
- Kedves, M. (1986a): Introduction to the Palynology of pre-Quaternary deposits. Part I. Studia Biol. Acad. Sci. Hung. 19: 1-164.
- Kedves, M. (1986b): Introduction to the Palynology of pre-Quaternary deposits. Part II. Studia Biol. Acad. Sci. Hung. 20: 1-144.
- Kedves, M. (1986c): Dégradation expérimentale des colonies du genre Botryococcus des schistes pétrolifères du Tertiaire supérieur de Hongrie. Acta Biol. Szeged 32: 39-48.

- Kedves, M. (1986d): In vitro destruction of the exine of recent palynomorphs I. Acta Biol. Szeged 32: 49–60.
- Kedves, M. (1986e): Komplex (LM, TEM és vékonyréteg kromatográfiás) vizsgálatok olajpala növényi mikrofossziliáin. (Complex (LM, TEM and thin layer chromatography) studies on plant micro-fossiles of oil slate.) Bot. Közlem. 73: 25–32.
- Kedves, M., Diniz, F. (1983): Les Normapolles du Crétacé supérieur en Europe: Implications paléobiogéographiques. Géobios 16: 329–345.
- Kedves, M., Körmöczi, L. (1985): Sur les problèmes de conservation des sporomorphes dans des conditions différentes. An. Asoc. Palinol. Leng. Esp. 2: 263–271.
- Kedves, M., Párdutz, Á. (1970): Études palynologiques des couches du Tertiaire inférieur de la Région Parisienne VI. Ultrastructure de quelques pollens d'Angiospermes de l'Éocène inférieur. Pollen et Spores 12: 553–575.
- Kedves, M., Párdutz, Á. (1983): Electron microscope investigations of the early Normapolles pollen genus Atlantopollis. Palynology 7: 153–169.
- Kedves, M., Simoncsics, P. (1964): Microstratigraphy of the carbonate manganese ore layers of the shaft III of Úrkút on the basis of palynological investigations. Acta Miner.—Petr. 16: 3–48.
- Kriván-Hutter, E. (1961): A dorogi borókási-medencerész középsőeocén barnakőszén összletének palynológiai rétegtana. (Palynological layer-studies on the brown-coal deposits of the Middle-miocen in the borókás-basin near Dorog.) In Hungarian. Földt. Közl. 91: 32–43.
- Maác, G.J., Simoncsics, P. (1956): Braunkohlenuntersuchungen aus dem Kohlenrevier von Borsod. II. (Fortsetzung). Acta Biol. Szeged 2: 51–58.
- Miháلتz-Faragó, M. (1966): Palynological study of Lower Pannonian strata in the region of Görömböly. Acta Miner.—Petr. 17: 181–183.
- Miháلتz-Faragó, M. (1976): Az Egyek 1. sz. fúrás palinológiai vizsgálata. (Palynological analysis of the bore No. 1. of Egyek.) In Hungarian. MÁFI évi jelentése az 1973. évről: 219–231.
- Miháلتz-Faragó, M. (1979): A Kecskemét KE-3. sz. fúrás paleoflórája palinológiai vizsgálatok alapján. (The paleoflora of the bore KE-3. in Kecskemét based on palynological studies.) In Hungarian. MÁFI évi jelentése az 1977. évről: 153–162.
- Miháلتz-Faragó, M. (1982): Tiszántúli alapfúrások palinológiai vizsgálata. (Palynological study of the basic bores in the over Tisza region.) In Hungarian. MÁFI évi jelentése az 1980. évről: 103–120.
- Miháلتz-Faragó, M., Mucsi, M. (1971): Geologische Entwicklungsgeschichte von Natronteichen auf Grund palynologische Untersuchungen. Acta Geogr. Szeged 11: 93–101.
- Nagy, E. (1957): A mátraalji felsőpannóniai barnakőszén rétegek pollenvizsgálata. (Palynological analysis of Upper-Pannonian brown-coal layers at the foot of Mátra Mountains.) In Hungarian. Földt. Közl. 87: 320–324.
- Nagy, E. (1958): A mátraalji felső-pannóniai korú barnakőszén palinológiai vizsgálata. (Palynological analysis of the Upper-Pannonian brown coal of the Mátra foothills.) In Hungarian. Földt. Int. Évk. 47: 3–143.

- Nagy, E. (1959): Pollenanalytische Untersuchungen einer ungarischen pliozänen Braunkohle. Acta Bot. Acad. Sci. Hung. 5: 413-423.
- Nagy, E. (1960): Gyors kiértékelési módszer alkalmazása a magyar palynológiában. (Quick method for evaluating in the Hungarian palynology.) In Hungarian. MÁFI évi jelentése az 1959. évről: 415-423.
- Nagy, E. (1962): Reconstructions of vegetation from the Miocene sediments of the Eastern Mecsek Mountains on the strength of palynological investigations. Acta Bot. Acad. Sci. Hung. 8: 319-328.
- Nagy, E. (1963): Some new spore and pollen species from the Neogene of the Mecsek Mountains. Acta Bot. Acad. Sci. Hung. 9: 387-404.
- Nagy, E. (1963b): Spores et pollen nouveaux d'une coupe de la briqueterie d'Eger (Hongrie). Pollen et Spores 5: 397-412.
- Nagy, E. (1963c): Occurrence of the genus Ephedripites in the Neogene of Hungary. Grana Palynologica 4: 277-280.
- Nagy, E. (1965): The microplankton occurring in the Neogene of the Mecsek Mountains. Acta Bot. Acad. Sci. Hung. 11: 197-216.
- Nagy, E. (1966): Investigations into the neogenic microplankton of Hungary. Paleobotanist 15: 38-46.
- Nagy, E. (1967): Palynological study of the Neogene deposits of the Mecsek Mountains (Hungary). Palaeogeogr. Palaeoclimatol., Palaeoecol. 3: 111-120.
- Nagy, E. (1968): Moss spores in Hungarian Neogene strata. Acta Bot. Acad. Sci. Hung. 14: 113-132.
- Nagy, E. (1969): A Mecsek hegység miocén rétegeinek palynológiai vizsgálata. (Palynological study of the Miocene layers of the Mecsek Mountains.) In Hungarian. MÁFI Évkönyve 52: 237-648.
- Nagy, E. (1973): Palynological data for the Neogene of Cserehát. Acta Bot. Acad. Sci. Hung. 19: 453-460.
- Nagy, E. (1976a): Paleoflóra változások a magyarországi palynológiai vizsgálatok alapján. (Changes of the paleoflora based on palynological studies in Hungary.) In Hungarian. Földt. Közl. 106: 177-180.
- Nagy, E. (1976b): A dunántúli olajpala-kutató fúrások rétegsorának palinológiai vizsgálata. (Palynological analysis of the Transdanubian oil-slate layers.) In Hungarian. MÁFI évi jelentése az 1974. évről: 247-261.
- Nagy, E. (1979a): Palynological evaluation of the holostratotype of the Egerian. Acta Biol. Szeged 25: 45-52.
- Nagy, E. (1979b): New tropical elements from the Hungarian Neogene. Grana 18: 183-188.
- Nagy, E. (1980): Palynological data of the Neogene marginal facies in Hungary. IV. Int. Palynol. Conf., Lucknow (1976-77) 2: 444-449.
- Nagy, E. (1985): A magyarországi neogén sporomorfái. (The sporomorpha of the Hungarian Neogene.) In Hungarian. Geol. Hung. 47: 1-471.
- Nagy-Bodor, E. (1982): A Tengelici 2. sz. fúrás miocén palynomorfái. (The Miocene palynomorpha of the bore No. 2. of Tengelici.) In Hungarian. MÁFI évkönyve 65: 117-138.

- Osváth, P., Balázs, I., Simoncsics, P. (1970): A levegő pollentartalmának és gombaszámának változása. Összefüggések az asztmás rohamok jelentkezésével. (Changes in the pollen content and number of mycospores in the air. Their correlations to asthmatic attacks.) In Hungarian. Rheumatologia-Balneologia-Allergologia 11: 178-183.
- Pálfi, G., Gulyás, S. (1985): Rapid determination of pollen fertility of two insect pollinated plant species by staining with the aid of proline-isatin reaction. Acta Biol. Szeged 31: 49-53.
- Pálfi, G., Köves, E. (1984): Determination of vitality of pollen on the basis its amino acid content. Biochem. Physiol. Pflz. 179: 237-240.
- Pálfi, G., Pálfi, Zs. (1982): A rapid method for the determination of fertility of maize pollen with the prolineisatin reaction. Maydica. 27: 107-111.
- Rákosi, L. (1966): A Szentendre 2. sz. fúrás palynológiai vizsgálata. (Palynological analysis of the bore No. 2. of Szentendre.) In Hungarian. MÁFI évi jelentése az 1966. évről: 377-387.
- Rákosi, L. (1968): A Csehbánya 1. sz. és a Balinka 252 sz. fúrás alsóeocén rétegeinek palynológiai szintézise. (Palynological synthesis about the Lower-Eocene layers of the bores Csehbánya No. 1 and Balinka No.252.) In Hungarian. MÁFI évi jelentése az 1966. évről: 83-94.
- Rákosi, L. (1970): A dorogi barnaköszénmedence Neokom fekvőrétegeinek palynológiai vizsgálata. (Palynological analysis of the Neokom-layers of the brown-coal basin of Dorog.) In Hungarian. MÁFI évi jelentése az 1968. évről: 267-292.
- Rákosi, L. (1971): Les associations de la végétation Eocene du Bassin lignitifère de Dorog. Ann. Inst. Geol. Publ. Hung. 54: 265-272.
- Rákosi, L. (1973): A Dorogi-medence paleogén képződményeinek palinológiája. (Palynology of the Paleogene fossils of the Dorog-Basin.) In Hungarian. MÁFI évkönyve 55: 500-575.
- Rákosi, L. (1977): A nagygyházi terület bauxit és áthalmazott dolomitösszetételének kormeghatározása palinológiai alapon. (Age determination of the transferred dolomite and bauxite layers of Nagygyháza palynological basis.) In Hungarian. MÁFI évi jelentése az 1975. évről: 283-293.
- Rákosi, L. (1978): A magyarországi eocén mangrove meghatározása palinológiai alapon. (Determination of the Hungarian Eocene-mangrove on palynological basis.) In Hungarian. MÁFI évi jelentése az 1976. évről: 358-374.
- Rákosi, L. (1979): A Dunántúli-Középhegység eocén képződményeinek biozónái palinológiai vizsgálatok alapján. (Biozones of Eocene fossils in the Transdanubian Middle Range based on palynological analyses.) In Hungarian. MÁFI évi jelentése az 1977. évről: 241-256.
- Rákosi, L. (1980): Az eocén-oligocén határkérdés a palinológiai vizsgálatok alapján. (The problem of the Eocene-Oligocene border on palynological basis.) In Hungarian. Űslénytani Viták 25: 117-125.
- Rákosi, L. (1983): A dorogi barnaköszén-medence Kerek-dombi kutatási területének palynológiai vizsgálata. (Palynological analysis of the Kerek-domb area of the brown-coal basin of Dorog.) In Hungarian. MÁFI évi jelentése az 1981. évről: 327-334.

- Rákosi, L., Tóth, K. (1980): Adatok a Déli-Bakony eocén képződményeinek lito- és biosztratigráfiájához. (Data to the litho- and biostratigraphy of the Eocene fossils in the South-Bakony Mountains.) In Hungarian. MÁFI évi jelentése az 1978. évről, 239–261.
- Rowley, J.R., Járai-Komlódi, M. (1976): Observation of one pollen grain by SEM, TEM and light microscopy. Acta Bot. Acad. Sci. Hung. 22: 449–461.
- Siegl-Farkas, Á. (1983): A Magyarpolányi Szenon képződményeinek palynológiája. (Palynology of the Senonian fossils of Magyarpolány.) In Hungarian. Őslénytani Viták 29: 59–69.
- Siegl-Farkas, Á. (1984): Az Upponyi hegység rejső-kréta képződményeinek palynostratigráfiája. (Palynostratigraphy of the Upper-Cretaceous fossils of the Upponyi Mountains.) In Hungarian. MÁFI évi jelentése az 1982. évről: 101–117.
- Siegl-Farkas, Á. (1985): A Zalagyömrő-Gyepűkajáni terület szenon képződményeinek palynostratigráfiája. (Palynostratigraphy of the Senonian fossils of the Zalagyömrő-Gyepűkaján area.) In Hungarian. MÁFI évi jelentése az 1983. évről: 213–218.
- Simoncsics, P. (1959): Palynologische Untersuchungen an der miozänen Braunkohle des Salgótarjáner Kohlenreviers I. Die Sporomorphen-Flora von Katalinbánya. Acta Biol. Szeged 5: 181–199.
- Simoncsics, P. (1960): Palynologische Untersuchungen an der miozänen Braunkohlen des Salgótarjáner Kohlenreviers. II. Sukzession der Pflanzenvereine des Miozänmoores von Katalinbánya. Acta Biol. Szeged 6: 99–106.
- Simoncsics, P. (1963): Palynologische Untersuchung der Neogenen Kernbohrung von Damak (Nordostungarn). Grana Palynologica 4: 410–423.
- Simoncsics, P. (1969): Sporen- Pollen- und Moortypen aus dem Miozänen Braunkohlenggebiet von Nógrád I. Acta Biol. Szeged 15: 37–49.
- Simoncsics, P., Kedves, M. (1961): Paleobotanical examinations on manganese series in Úrkút (Hungary, Transdanubia). Acta Miner.-Petr. 14: 27–57.
- Simoncsics, P., Osváth, P., Balázs, I. (1970): A levegő pollen-tartalmának quantitativ vizsgálata. (Quantitative analysis of the pollen-content in the air.) In Hungarian. Rheumatologia-Balneologia-Allergologia 11: 117–122.
- Soó, R. (1926): Die Entstehung der ungarischen Puszta. Ungarische Jahrbücher 6: 258–276.
- Stuhl, Á. (1962): A Balatonfelvidék perm időszaki üledékeiben végzett spóravizsgálatok eredményei. (Spore studies on the Permian sediments of the Balaton Highland.) In Hungarian. Földt. Közl. 91: 405–412.
- Sütő-Szentai, M. (1983): Az északkeleti Mecsek andezit fekvésében levő neogénképződmények palynológiai vizsgálata. (Palynological study on the Neogene fossils found in the andezite layers of the Northeastern Mecsek Mountains.) In Hungarian. Földtani Kutatás 26: 99–102.
- Szabó, M., Gulyás, S., Frank, J. (1984): Comparative anatomy of the androecium of male sterile and fertile sunflowers (*Helianthus*). Acta Bot. Hung. 30: 67–73.
- Szalay, I. (1943): A Hargita két tőzeglápjának virágporelemzése. (Palynological analysis of two peat bogs of the Hargita Mountains.) In Hungarian. Acta Bot. Univ. Szeged 2: 63–102.

- Tompa-Kashirskaya, A., Kozma, P. (1978): A szőlőpollen tanulmányozása scanning elektronmikroszkóppal. (Scanning-electronmicroscopic studies on grape-pollens.) In Hungarian. Kertészeti Egyet. Közl. 42: 25–39.
- Tompa-Kashirskaya, A., Kozma, P. (1981): Földrajzi-ökológiai szőlőfajtacsoportok pollenjének scanning elektronmikroszkopikus tulajdonságai. (Scanning-electronmicroscopic characters of the pollen grains of different geographical-ecological grape-sort groups.) In Hungarian. Kertészeti Egyet. Közl. 45: 93–100.
- Venkatachala, B.S., Góczán, F. (1964): The spore-pollen flora of the Hungarian "Kössen Facies". Acta Geol. 8: 203–228.
- Vozáry, E. (1957): Pollenanalytische Untersuchung des Torfmoores "Nyírestó" in Nordosten der Ungarischen Tiefebene (Alföld). Acta Bot. Acad. Sci. Hung. 3: 123–134.
- Zólyomi, B. (1931): A Bükk-hegység környékének Sphagnum lápjai. (Vegetationsstudien an den Sphagnum-mooren um das Bükkgebirge in Mittelungarn.) Bot. Közl. 28: 89–121.
- Zólyomi, B. (1936): Tízezer év története virágporszemekben. (Ten thousand year history in pollen grains.) In Hungarian. Term. Tud. Közl. 66: 504–516.
- Zólyomi, B. (1937): Pollenelemzési vizsgálatok a Rákospatak völgyében. (Pollenanalytische Untersuchungen im Tal des Rákos-Baches.) Bot. Közl. 34: 82, 84.
- Zólyomi, B. (1952): Magyarország növénytakarójának fejlődéstörténete az utolsó jégkorszaktól. MTA Biol. Oszt. Közlem. 1: 491–530. Die Entwicklungsgeschichte der Vegetation Ungarns seit dem letzten Interglazial. Acta Biol. Acad. Sci. Hung. 4: 367–430 (1953).
- Zólyomi, B., Précsényi, I. (1985): Pollenstatistische Analyse der Teichablagerungen des mittelalterlichen Klosters bei Pilisszentkereszt. Acta Archaeologica Acad. Sci. Hung. 37: 153–158.

PALYNOLOGY OF THE PANNONIAN AND PONTIAN OF HUNGARY

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A brief summary of the results of palynological researches on the Hungarian Pannonian and Pontian is given by the author. The vegetation is characterized by regional units. Finally the climatic distribution of the vegetation in the most characteristic boreholes is shown in detail.

I.

Comprehensive palynological evaluation of the Hungarian s. l. Pannonian (Pannonian and Pontian or Lower- and Upper-Pannonian) has not been made so far. The Mátraalja Upper-Pannonian monograph (NAGY 1958) was the first work on Pliocene palynology in Hungary. The subject of subsequent investigations was — in general — the palynology of the Neogene in Hungary, and in the framework of this, Pannonian and Pontian strata were also explored. The latter was either described in papers specially on the Pannonian and Pontian (NAGY: The Transdanubian oil shale 1976, 1977; Palynofacies in the Hungarian Pannonian 1983, 1984; NAGY et PÁLFALVY: Rudabánya 1961), or works dealing with the Neogene included a palynological evaluation of the Pannonian and Pontian strata (NAGY 1960, 1967, 1968, 1969, 1970, 1971, 1976). Further papers on Pannonian and Pontian palynology were published in Hungary by KEDVES 1962, RÁKOSI 1963, BÓNA et SZENTAI 1966, FARAGÓ 1975, PÁLFALVY et RÁKOSI 1979, SZENTAI 1982, BODOR 1983. All this work completed with the so far unpublished investigations — in short: the Hungarian Pannonian and Pontian stage (s. l. Pannonian) can be characterized as follows.

II.

The palynological data mostly served for geological mapping and generally were obtained through the evaluation of bore samples. To a minor extent,

however, materials of explorations, outcrops, mine profiles were also processed. Most of the data are from localities on the borders of the Hungarian basin, only a small proportion from its central part, far from the borders. (Map (localities), Fig. 1).



Fig. 1. Sketch of the important localities

III.

The Pannonian samples from the borehole Hidas 53, in the south-eastern part of the present Transdanubia, north-east of the Mecsek-Mountains are indicative of a brackish-water inland sea origin. In the coastal region of the Pannonian inland sea the existence of smaller Taxodiaceae marsh- or swamp forest, then fresh water can be concluded on even from the presence of the pollen grains of Nuphar. Remains (Carya, Alnus, Betula) indicative of the presence of fernery and deciduous forests preferring warm-temperate or subtropical climates on the shore of the fresh water were also found. Farther from the shore mixed deciduous forests requiring a drier, warm-temperate climate (Ulmus, Zelkova, Celtis, Tilia, Juglans) grew. Abies and Picea species indicative of higher belts were associated with Keteleeria, Tsuga, Cedrus and Podocarpus, species living today in subtropical mountains.

The one-time mother plants for Pinus pollen grains which are encountered in extremely large quantities may have lived in the mixed deciduous forests and in forest stands of higher mountain slopes alike.

Samples from the same area representing the lower and medium part of the Pontian are also of brackish-water origin as proved by the presence of Dinoflagellatae, though beside them fresh-water algae (Spirogyra, Botryococcus) occur as well. Pollen grains indicative of marsh-, moist belt- and fresh-water vegetation (Taxodiaceae, Cupressaceae, Myrica, Myriophyllum and Sparganium) are scarce. Spores of mosses and ferns (Encalyptaesporites pliocenicus, Laevigatosporites haardtii) are found in rather large quantities. These were joined by Compositae as undergrowth. Species of fresh-water shores were: Carya, Pterocarya, Alnus, Betula, Salix, Liquidambar, then representatives of drier forests: Ulmus, Zelkova, some Quercus, Fagus, Carpinus.

The dominant coniferous pollen grains are indicative of mountain- or mountain-slopes forests with the species Pinus, Picea, Abies, Tsuga, Cedrus, Keteleeria and a few Podocarpus.

On the north-western foothills of the Bakony-Mountains in the borehole Pápa 2, the lowermost part of the Pannonian is characterized by Cooksonella circularis, a species indicative of brackish-water, and by a mesozoic redeposition, then higher upwards by a rich brackish-water plankton stand (Dinoflagellata, Spirogyra etc.). In the upper part of the Pannonian the pollen grains are indicative of some subtropical fens, fresh water, and deciduous riparian forests. The existence of a drier warm-temperate forest on an area farther from the one-time shore is proved by a rich pollen material. The coniferous stand is poor, supposedly due to the direction of wind which was similar to that prevailing today (North-West). In the Pontian a few Dinoflagellatae associated with Spirogyra- and Botryococcus algae can be detected. The Sparganium pollen is indicative of fresh water. The area has features of open-sea facies not so much as the area at the northern foot of the Mecsek-Mountains.

The sporomorph community with the dominance of Coniferae is indicative of mountain-slopes- or mountain forests, of mixed deciduous forests with a demand for warm-temperate climate.

In a number of boreholes characteristic of the Pannonian of the western foothills of Gerecse — Tata (TV G) 26, 27, 29, Naszály 1 — the sometimes dominant appearance of a large number of plankton belonging to the range of form of Tectatodinium Wall 1967 can be demonstrated beside the

presence of a small number of Dinoflagellata occurring on the foothills of the Mecsek and Bakony. This indicates an ecological character different from those of the other areas. Here too, the subtropical Taxodium swamp- and marsh forest can be detected in the pollen spectra. Fresh-water hair-weed-, and water-side herbaceous- and alder communities with subtropical warm-temperate elements consistently show up. On inland areas farther from the sea rich, warm-temperate mixed forests might have lived. The undergrowth is rich: ferns, herbaceous plants, Polygonum, Compositae, as well as Corylus, Ostrya, Rhus and Lonicera are equally detected here. Here is, again, a great diversity of Coniferae: along with pollen of the dominant species Pinus, Abies, Picea, Keteleeria, Cedrus, Tsuga, those of Podocarpidites sp. can be found.

In boreholes sunk in several places of Transdanubia; in the southern part of the Bakony (boreholes Pula 3 and Várkesző 1) and on Kemeneshát on the North-West (borehole Gércse 1) — under peculiar palaeogeographic conditions in crater lakes — extraordinary ecological conditions are found to have developed in the Pontian. Alga colonies of Botryococcus braunii Kützg. often accumulated in rock-forming volumes in them (JÁMBOR Á., SOLTÍ G. 1971). The spore- and pollen spectra are indicative of Pontian with a rich vegetation of Coniferae as dominant species and some marsh- and/or swamp-forest elements. In these alginites the warm-temperate elements are sub-dominant (Fig. 2).

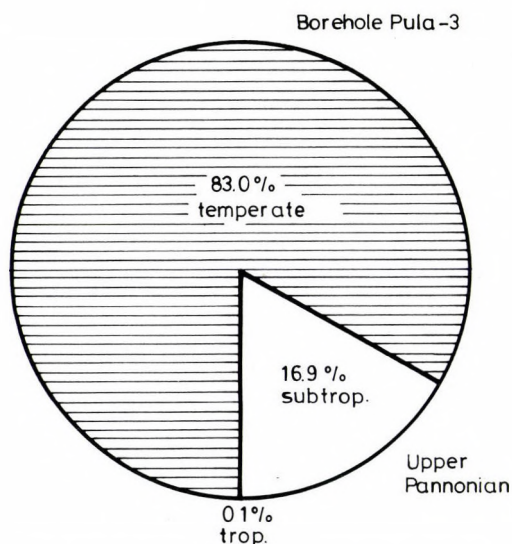


Fig. 2. The climatic distribution of the vegetation in the borehole Pula 3

According to the evidence of borehole Tököl 1 the north-western marginal region of the Great Hungarian Plain must have been an inland sea at the time of the Pannonian, as suggested by the brackish-water community of Dinoflagellatae and Hystrichosphaeridae. They were joined by Pleurozonaria and Hidasia species. The coast may have been bordered by fresh-water swamp- and/or marshforest. Along the fresh-water course moisture demanding deciduous forests were associated with ferns. The mixed deciduous forest (with Tilia, Ulmus, Zelkova, Juglans, Acer, Carpinus species) on the drier areas farther from the banks is indicative of a moderately warm climate. The shrubs (Corylus, Ostrya, Ericaceae, Eleagnaceae, Caprifoliaceae etc.) must have preferred a similar warm-temperate climate. Coniferae are dominant species here too, with characteristic warm-temperate and subtropical elements.

Samples from the same area — from the Pontian outcrops-layer of the Kőbánya brick-yard — gave palynologically evaluable spectra only for the lower part of the Pontian. The plankton organisms mostly are of brackish-water origin. Besides them, however, the presence of fresh-water is also proved by a few fresh-water plankton organisms and pollen grains from some fresh-water plants. Subtropical marsh- and swampforest is indicated only by a small quantity of Taxodiaceae pollen grains, still, with the presence of Nyssa and Jussiaea their one-time existence is made probable. The picture is completed by pollen grains indicative of warm-temperate deciduous forests, and dominantly by those of Coniferae with airbladders.

In the upper — still valuable — sections of the profiles a retreat of subtropical elements and advance of warm-temperate deciduous forests can be observed.

In boreholes sunk in the northern and north-eastern part of the Great Hungarian Plain the lower and upper part of the Pontian can be detected. By the plankton organisms a brackish-water and a fresh-water stage can be differentiated. In the so-called oscillation stage of the Pontian fresh-water-, marsh- and swamp forest communities alternated. Then the border of Pliocene and Pleistocene is borehole Jászládány 1 is characterized by fresh-water plankton organisms and herbaceous plants. Elements of water-side with Alnus, pollen grains from a few Coniferae — mainly from Pinus — indicative of warm-temperate deciduous- and mountain forests make the picture complete.

The lignite mine at Mátraalja, Petőfi-bánya and surface mine at Vison-ta, and at the foot of the Bükk as well as the lignite borehole at Torony,

Western Transdanubia can be compared for the Pontian oscillation stage with the ecological communities of *Taxodium* swamp- and marsh-forest.

In the hill-country of Szerencs in North-Hungary (borehole Megyaszó 1) in strata proved Pannonian — by the presence of *Ostracodae-Spirogyra* sp., *Botryococcus braunii*, plankton organisms (*Monogemmites setarius* of uncertain origin) belonging to the range of form of *Leiosphaeridae* are found. Sub-tropical swamp- and marsh-forest, warm-temperate fresh-water communities can also be detected there. The mixed deciduous forest of a drier horizon was very rich in species. Its undergrowth contained positively subtropical and warm-temperate elements (*Palmae* and *Reevesia*). *Coniferae* are dominant; here — like in other parts of Hungary — subtropical species (*Ginkgo*, *Cedrus*, *Tsuga*, *Podocarpus*) are also found.

The Pontian stage of the borehole is characterized by fresh-water plankton organisms and fresh-water plants. The spectra is made complete by swamp- and marshforest, warm-temperate mixed deciduous forest and a rich coniferous stand.

In the Pannonian material of the borehole Alsóvadász 1 explored on the area of Cserehát, besides the uncertain origin *Monogemmites setarius* only the *Botryococcus braunii* alga indicates the fresh-water inland lake. Fresh-water is indicated by the presence of *Trapa* as well. In the case of the retreating inland lake swamp — and/or marshforest were natural phenomena. The undergrowth of the drier mixed deciduous forest, farther in from the riparian forest is indicative of a moderately warm climate with occasional drought resistant elements (*Ephedra*, *Ilex*). Subtropical elements were scarce. A few *Gramineae*, *Chenopodiaceae*, *Amaranthaceae* and some *Compositae* must have formed the undergrowth.

According to the palynological analyses samples from the Debréte 1 and other boreholes in the northern border region of Hungary, on the northern side of the Bükk-Mountains represent the Pontian. Along with remains of fresh-water plankton, fresh-water herbaceous plants and water-side plants those of a warm-temperate deciduous forest rich in species (*Celtis*, *Ostrya*, *Rhus*, *Liquidambar*, *Pterocarya*) can be detected. *Fagus* pollens are of dominant character, and coniferous species continue to be similarly dominant.

IV.

To sum it all up: The pollen diagrams for the Pannonian and Pontian generally are characterized by the dominance of *Coniferae*. Characteristic

is, further, the infrequent occurrence of tropical elements. In the Pannonian very few Sapotaceae, palmae (palaeotropical species) and/or Jussiaea (neotropical species) are encountered. In the Pontian the few tropical species are mostly confined to the carbonaceous complexes. The number of subtropical elements greatly varies according to the situation of the locality and its distance from the shore. Characteristic changes in the flora elements of some major localities are shown in diagrams.

In the Mecsek-Mountains (borehole Hidas 53) the quantity of tropical elements in the Pannonian and Pontian is more or less the same. Owing to the southern character of the area, under the influence of the inland sea the climate was balanced. The diagrams are characterized by the dominance of warm-temperate flora elements from the nearby mountains. The upper part of the Pontian is not contained in the range of strata examined (Fig. 3).

In the northern part of Transdanubia (borehole Naszály 1) the ratio of tropical elements in the Pannonian and Pontian is nearly identical. The oscillation stage is again absent (Fig. 4).

In the Pannonian of the borehole Megyaszó 1 sunk on the area of the Szerencs-hill country some tropical elements can be detected unlike in the Pontian where the carbonaceous facies has not been examined, and only an increase in the number of subtropical elements allows drawing conclusions (Fig. 5).

A great advance of subtropical elements can be demonstrated for the time of lignite formation at Mátraalja by the diagram of Taxodiaceae swamp- and marsh-forest (Fig. 6).

Finally, boreholes sunk north of the Bükk-Mountains do not contain tropical elements. Subtropical remains are considerable, but the presence and amount of Fagus pollen from a temperate zone vegetation is remarkable (Fig. 7).

The inland lake played an important role in shaping the climate, first of all in balancing it; it must have been a warm-temperate, mediterranean climate. In consequence of the retreat then disappearance of the inland lake, the upper part of the Pontian must have been characterized by a more continental climate and the prevalence of local climates.

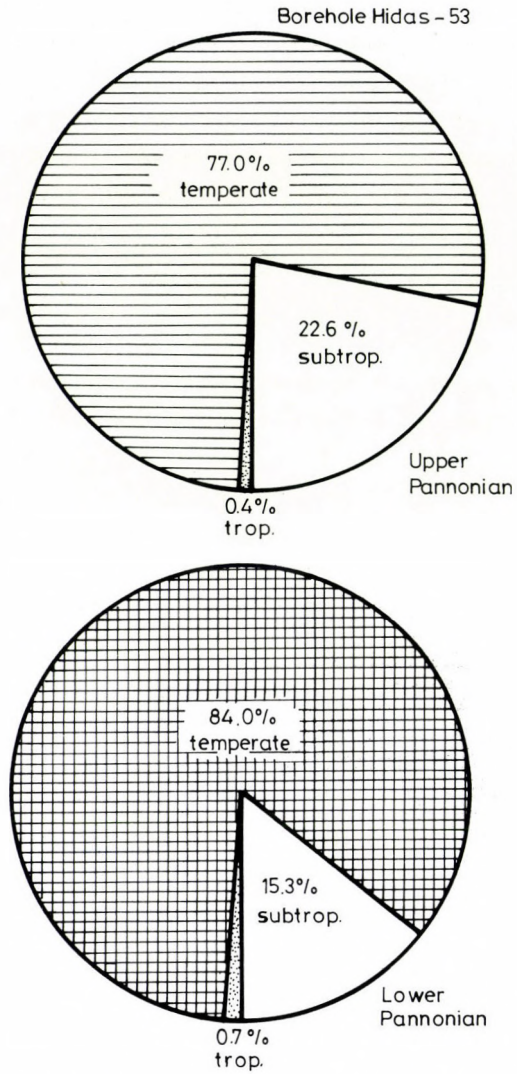


Fig. 3. The climatic distribution of the vegetation in the borehole Hidas 53

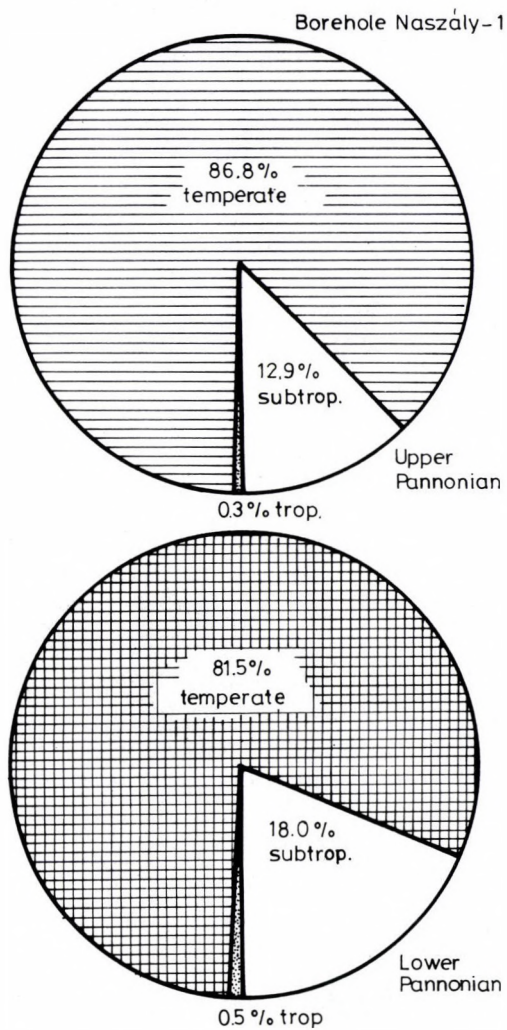


Fig. 4. The climatic distribution of the vegetation in the borehole Naszály 1

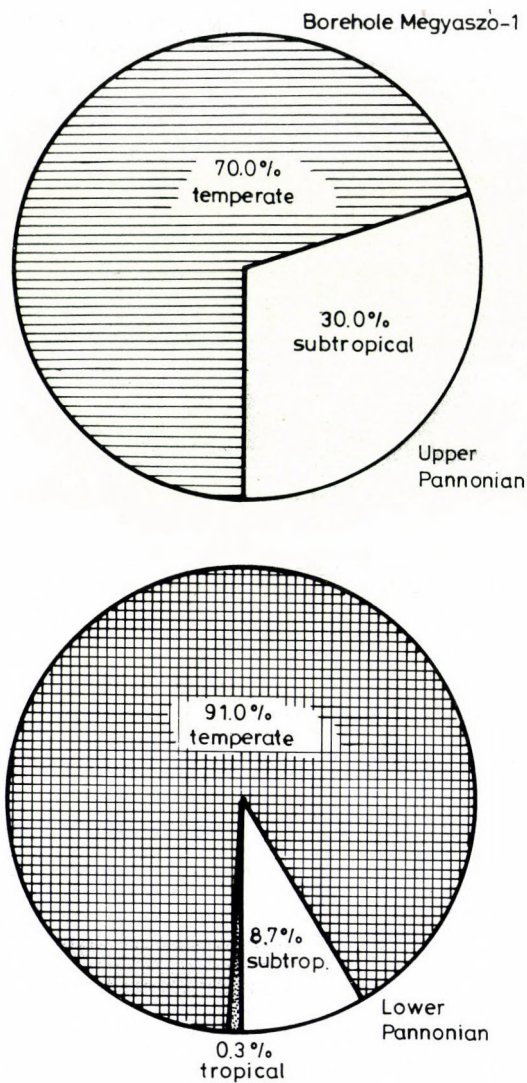


Fig. 5. The climatic distribution of the vegetation in the borehole Megyaszo 1

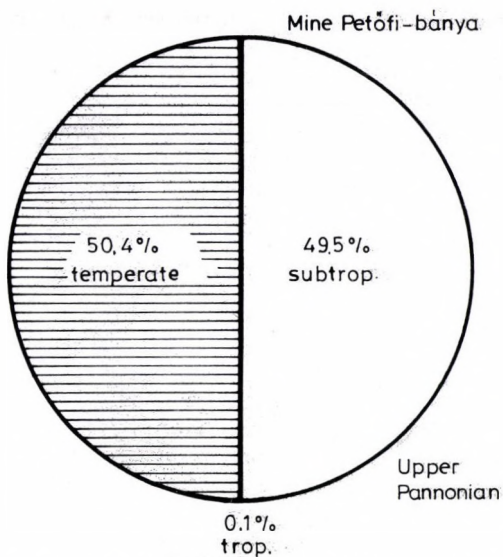


Fig. 6. The climatic distribution of the vegetation in the mine Petőfi-bánya

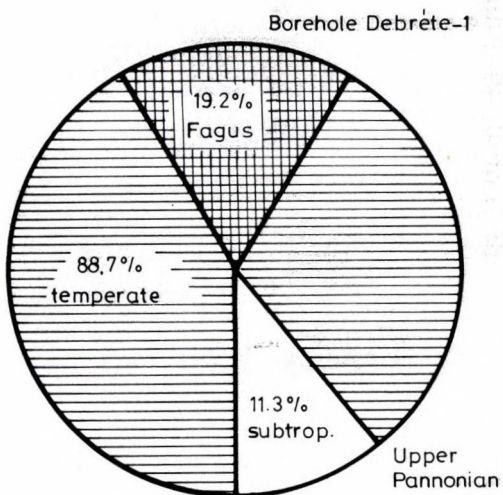


Fig. 7. The climatic distribution of the vegetation in the borehole Debréte 1

REFERENCES

- Baltes, N. (1971): Tertiary plant microfossil assemblages from the Pannonian depression (Rumania) and their palaeoecology. — Rev. Palaeobot. Palyn. 11: 125–158. Utrecht.
- Bartha, F. (1971): A magyarországi pannon biosztratigráfiai vizsgálata. (Biostratigraphical analysis of the Pannonian in Hungary.) In Hungarian. Akadémiai Kiadó, Budapest. pp. 9–172.
- Bodor, E. (1983): A Jánoshalmi l. sz. alapfúrás palynológiai vizsgálata. (Palynological analysis of the bore No. 1. of Jánoshalma.) In Hungarian. Acta Geogr. Geol. Mineral. Debrecina 1982. 21. 135–159.
- Bóna, J., Rumliné, Szentai, M. (1966): A mátraaljai lignitkutató fúrások palynológiai eredményei. — Palynologische Ergebnisse der Erkundungsbohrungen auf Lignit in Mátraalja. — Földt. Közlöny 96/4: 421–426.
- Jámbor Á., Solti G. (1976): A Balatonfelvidéken és a Kemenesháton felkutatott felsőpannoniai olajpala előfordulás földtani viszonyai. — Geological conditions of the Upper Pannonian oil – shale deposit recovered in the Balaton Highland and at Kemeneshát (Transdanubia, Hungary). — MÁFI Évi Jel. az 1974. évről. 193–219.
- Kedves M. (1962): Palynologic investigation on coals of the Upper Pannonian I. — Acta Biol. Szeged. N.S. VIII: 77–81.
- Nagy E. (1958): A mátraaljai felső pannóniai korú barnakőszén palynológiai vizsgálata. — Palynologische Untersuchung der am Fusse des Mátragebirges gelagerten Oberpannonischen Braunkohle. — MÁFI ÉVKÖNYV 47. 1. 1–353. Budapest, Műszaki Kiadó.
- Nagy E. (1960): The application of a method rapid evaluation in Hungarian Palynology. — Acta Univ. Szeged. Acta Biol. Nova Ser. VI: 91–97.
- Nagy E. (1962): Reconstructions of vegetation from the Miocene sediments of the Eastern Mecsek Mountains of the strength of palynological investigations. — Acta Bot. Acad. Sci. Hung. 8: 319–328. Budapest.
- Nagy E. (1967): Palynological study of the Neogene deposits of the Mecsek Mountains (Hungary). — Palaeogeography, Palaeoclimatology, Palaeoecology, 3: 111–120.
- Nagy E. (1968): Moss Spores in Hungarian Neogene Strata. — Acta Bot. Acad. Sci. Hung. 14: 113–132.
- Nagy E. (1969): A Mecsek hegység miocén rétegeinek palynológiai vizsgálata. — Palynological elaborations of the Miocene layers of the Mecsek Mountains. — MÁFI Évkönyv 52: 1–417 (232–649).
- Nagy E. (1970): Hungary's Neogene climate on the basis of palynological researches. — Com. on Mediter. Neog. Strat. Proceed. of the fourth Sess. in Bologna. — 19–30. Sep. 1967. L.I. Giornale di Geologia ser. 2a XXXV: 1.
- Nagy, E. (1971): Vergleichende palynologische Untersuchungen im ungarischen Neogen. — Földt. Közlöny, Bull. of the Hungarian Geol. Soc. 101: 244–246. (Coll. on the Neogene, Budapest, 1969. 4–9. Sep.)
- Nagy, E. (1976): Paleoflóra változások a magyarországi neogénben palynológiai vizsgálatok alapján. (Changes of the paleoflora in the Neogene of Hungary based on palynological studies.) In Hungarian. Földt. Közlöny, Bull. of the Hungarian Geol. Soc. 106: 177–180.

- Nagy, E. (1976): Palynological investigation of Transdanubian oil shale exploratory boreholes (In Hungarian, English summary). — MÁFI Évi Jel. az 1974. évről. 247–261. Budapest.
- Nagy, E. (1984): Palynofacies in the Hungarian Pannonian s.l. L. Roth 1879. — Paleobiologie continentale, Montpellier, XIV. No. 2. 371–376.
- Miháltzné Faragó, M. (1976): Az Egyek 1. sz. fúrás palynológiai vizsgálata. — Palynological analysis of borehole Egyek-1. — MÁFI Évi Jel. 1973. évről. 119–231.
- Pálfalvy, I. — Rákosi, L. (1979): A visontai lignittelepes összlet növénymaradványai. — Die Pflanzenreste des lignitflözführenden Komplexes von Visonta (N.-Ungarn). — MÁFI Évi Jel. az 1977. évről. 47–66.
- Petrescu, I., E. Nicorici, Fr. Wanek, I. Blidaru (1979): Date biostratigraphice cu privire la neogenul din forajul hidrogeologic de la Oradea — Est (F₁A). — Nymphaea, VII: 111–129. Oradea.
- Planderová, É. (1962): Bemerkungen zur Entwicklung der Flora und zu den klimatischen Veränderungen im Neogen der SW Slowakei — Geol. práce, 63: 147–156. (Slowakisch mit deutscher Zusammenfassung.).
- Planderová, É. (1972): Pliocene sporomorphs from the West Carpathian Mountains and their stratigraphic interpretation. — Geologické práce Zpráva 59: 209–283. Bratislava.
- Rákosi, L. (1963): Bükkábrány 15/8. sz. fúrás palynológiai vizsgálata. (Palynological analysis of the bore No. 15/8. of Bükkábrány.) In Hungarian. Földtani Kutatás, VI/4. 24–30.
- Sütőné, Szentai, M. (1982): A Tengelice-2. sz. fúrás pannóniai képződményeinek szervesvázú mikroplankton és sporomorpha maradványai. — Organic mikroplanktonic and sporomorpha remains from the Pannonian from the borehole Tengelice-2. — MÁFI Évkönyv LXV: 205–233.

MICROPLANKTON ZONES OF ORGANIC SKELETON IN THE PANNONIAN S.l. STRATUM
COMPLEX AND IN THE UPPER PART OF THE SARMATIAN STRATA

MÁRIA SÜTŐ-SZENTAI

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The paper contains a description of the microplankton zones of organic skeleton. From the Pannonian s.l. stratum complex eight zones are described. They are: Mecsekia ultima, Spiniferites bentori pannonicus, Spiniferites bentori oblongus, Pontiadinium pécsváradensis, Spiniferites bentori coniunctus, Spiniferites validus, Dinoflagellata-Zygnemataceae, Mougeotia laetevirens. From the upper part of the Sarmatian strata the description of the Spiniferites bentori budajenőensis-Mecsekia incrassata zone is given. The development of the Pannonian microplankton communities and their origin from the Sarmatian communities are briefly touched upon. The vertical distribution of the zone marking communities is shown in a table (Table 1), the characteristic species are represented by photos.

INTRODUCTION

The organic skeleton microplankton study of the Pannonian s.l. stratum complex was started in 1979 in the Central Material Testing Laboratory of the National Geological Research and Boring Enterprise, on the order of the Hungarian State Institute for Geology. In past years more than thirty bore logs and some 2000 samples from various borings were examined. The aim of the examination was to describe the Dinoflagellatae, Zygnemataceae and other organic, supposedly alga remnants of unknown taxonomic place within the Pannonian s.l. stratum complex, determine their stratigraphical distribution and elaborate the zonation. The description of the microplankton community is in process, the zonation — apart from works of informative nature published so far — is described in some more detail in this paper.

The zonation in Transdanubia, in the Danube-Tisza Interfluve and on the southern border of the Northern Hungarian Middle Range was described from core samples obtained by sunken boring. The microplankton communities of the Sarmatian substrata were studied on samples obtained from boreholes where sedimentation towards the Pannonian strata was continuous and the transformation of the microplankton communities could be observed. This paper deals with the vertical distribution of the microplankton communities,

their horizontal relations and the descriptions of species go beyond the scope of this paper. Method of identification:

On dinoflagellatae characteristic of the Pannonian s.l. stratum complex the first information was supplied by Mrs. Esther NAGY (1965, 1966) who even described several species. After that Nicolae BALTES (1971a, b) described in a number of papers the roumanian so-called "pontian" Dinoflagellatae community and gave their stratigraphical distribution too. The community he described and showed in photos is identical with the communities of our Upper Pannonian Spiniferites balcanica main zone. In the meantime the conclusions of studies by David WALL and Barrie DALE (1968, 1970) reached us, with morphological descriptions and biological and ecological data concerning these Dinoflagellatae existing even today, which gave a guideline for our work. Besides them we relied on works by L.E. STOVER and W.R. EVITT (1978) as well as by J.K. LENTIN and G.L. WILLIAMS when identifying the communities.

THE UPPER PART OF THE SARMATIAN STAGE

Spiniferites bentori budajenőensis-Mecsekia incrassata zone

Typical locality: 1. Budajenő-No. 2 bore-hole 216-225 m Clayey marl aleurite; Other localities: 2. Pusztazámor-No. 2 bore-hole 80.2 m; 3. Lajoskomárom-No. 1, bore-hole 668.2-680.4 m; 4. Nagykozár-No. 2 bore-hole 292.3-293.4 m; 5. Szirák-No. 2/a. bore-hole 763.7-780 m; 6. Baktalórántháza-No. 1 bore-hole 1719.4-1721.7 m; 7. Vienna basin, Aderklaa-No. Tl. bore-hole 800.0 m (Fig. 1).

Characteristic community: Spiniferites bentori (Ross.) subsp. budajenőensis S.-Szentai and its variations, Spiniferites cf. bentori (Rossignol) Wall et Dale, Lingulodinium machaerophorum (Defl. et Cookson) Wall, Lingulodinium varium S.-Szentai, Polysphaeridium zoharyi (Rossignol) Bujak et al., Operculodinium centrocarpum (Defl. et Cookson) Wall, Hystrichosphaeropsis obscura Habib, Pterospermopsis cf. helios Sarjeant, Palaeocystodinium golzowense Alberti, Hidasia sp., Nematosphaeropsis sp., Chytroesphaeridia sp., Mecsekia spinosa Hajós, Mecsekia spinulosa Hajós, Mecsekia incrassata S.-Szentai, Mecsekia orientalis S.-Szentai, Cymatiosphaera nuda Hajós, Cymatiosphaera spinosa Hajós, Cymatiosphaera undulata Hajós, Cymatiosphaera sp., Botryococcus braunii Kützing Foraminifera (organic walled).

The environment of the Pusztazámor bore-hole with its relatively high

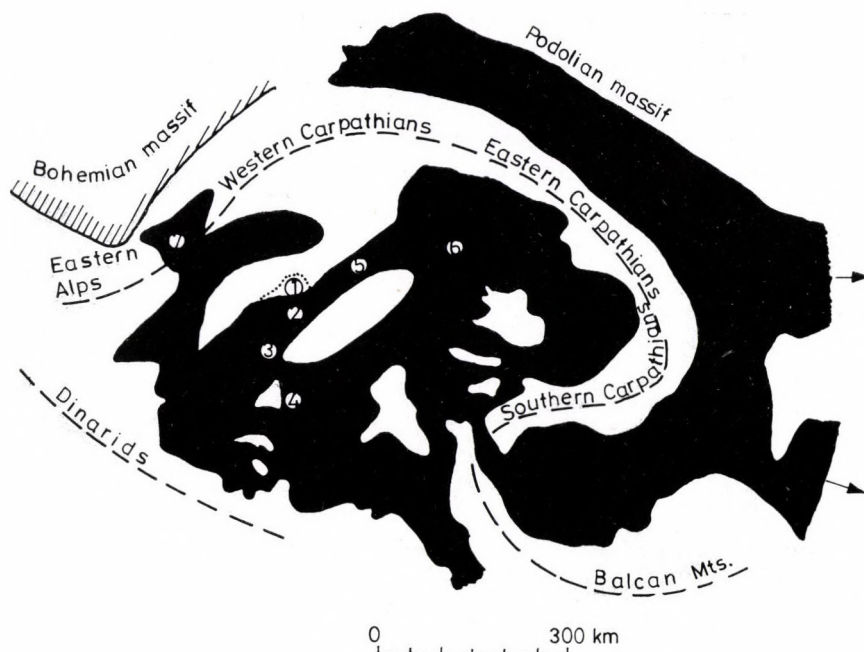


Fig. 1. Distribution of the medium Parathethys in the Sarmatian (B-D zone) after J. SENES 1972. Organic skeleton microplankton localities 1-7. For site (1) (Zsámbék basin) the original shoreline is corrected

salt content is characterized by the frequency of species from the genera Mecsekia and Cymatiosphaera. In the other bore logs the Lingulodinium species, Spiniferites cf. bentori, Hidasia sp. and the Mecsekia incrassata sp. are frequent. However, the frequency peaks of these species vary from sample to sample and are opposed to one another, supposedly because of differences in their ecological demands. The species Mecsekia incrassata runs over to the basic formations of the Pannonian strata, it is in our opinion this Mecsekia palaeoassociation that the species Mecsekia ultima developed.

In the upper part of the Sarmatian strata the subspecies Spiniferites bentori budajenöensis, a primitive form of the species S. bentori, is of rare occurrence. It may have formed in a palaeoassociation characterizable by Lingulodinium species and the species Spiniferites cf. bentori, from which the latter species developed further under the changed ecological conditions of the Pannonian inland sea.

Table 1

UPPER PART OF THE SAR- MATIAN STAGE	12	M. Y. (Jámbor Á. et al. 1985)							
	PANNONIAN s.l. STAGE					CLASSIFICATION BY AGE			
	LOWER PANNONIAN			UPPER PANNONIAN					
Mecsekia incrassata Spiniferites bentori budajenensis zone	Mecsekia ultima zone	Spiniferites bentori main zone			Spiniferites balcanica main zone		Dinoflagellata – Zygnemataceae közties zone	Mougeotia laetevirens zone	ORGANIC SKELETON MIKRO- PLANKTON ZONE
		Spiniferites bentori panmoni- cus zone	Spiniferites bentori oblongus zone	Pontadinium pécsváradensis zone	Spiniferites bentori coniunc- tus – S. para- doxus zone	Spiniferites validus zone			
									Spiniferites bentori budajenensis
									Spiniferites bentori budajenensis var.
									Spiniferites cf. bentori
									Lingulodinium machaerophorum
									Lingulodinium varium
									Polysphaeridium zoharyi
									Operculodinium centrocarpum
									Hystrichosphaeropsis obscura
									Nematosphaeropsis sp.
									Palaeocystodinium golzowense
									Pterospermopsis cf. helios
									Chytroeisphaeridia sp.
									Hidasia sp.
									Mecsekia spinosa
									Mecsekia spinulosa
									Mecsekia incrassata
									Mecsekia orientalis
									Cymatiosphaera nuda
									Cymatiosphaera spinosa
									Cymatiosphaer undulata
									Cymatiosphaera sp. indet.
									Hystrichosphaeridae (other forms)
									Pachisphaera pelagica
									Mecsekia ultima
									Spiniferites bentori pannonicus
									Spiniferites bentori granulatus
									Spiniferites bentori bentori
									Spiniferites bentori mátraensis
									Spiniferites bentori piriformis
									Spiniferites bentori var. truncata
									Spiniferites ramosus
									Spiniferites sp. (membranous forms)
									Gonyaulax digitale primus
									Gonyaulax digitale secundus
									Gonyaulax digitale tertius
									Dinoflagellata 70. form
									Dinoflagellata 71. form
									Dinoflagellata 72. form
									Spiniferites bentori oblongus
									Spiniferites sp.
									Spiniferites nodosus
									Nematosphaeropsis balcombiana
									Chytroeisphaeridia cariacensis
									Chytroeisphaeridia hungarica
									Dinoflagellata 129, 220 forms
									Gonyaulax digitale "pontiadinoid"
									Gonyaulax digitale quatuor
									Pontadinium pécsváradensis
									Pontadinium obseum
									Millioudodinium baltesi
									Millioudodinium lörentheyi
									Pontiadinium inequicornutum
									Spiniferites sp.
									Spiniferites nodosus
									Nematosphaeropsis balcombiana
									Chytroeisphaeridia cariacensis
									Chytroeisphaeridia hungarica
									Dinoflagellata 129, 220 forms
									Gonyaulax digitale "pontiadinoid"
									Gonyaulax digitale quatuor
									Pontadinium pécsváradensis
									Pontadinium obseum
									Millioudodinium baltesi
									Millioudodinium lörentheyi
									Pontiadinium inequicornutum
									Pontiadinium sp. (other forms)
									Spiniferites bentori coniunctus
									Spiniferites paradoxus
									Spiniferites balcanica
									Spiniferites tengelicensis
									Gonyaulax pannonicus
									Millioudodinium detkensis
									Millioudodinium foveolatum
									Millioudodinium pelagicum
									Millioudodinium jámbori
									Millioudodinium transdanuvianum
									Millioudodinium quadratum
									Impagidinium globosum
									Impagidinium spongianum
									Impagidinium cf. globosum
									Chytroeisphaeridia tuberosa
									Dinoflagellata 29. form
									Dinoflagellata 67. form
									Dinoflagellata (other forms)
									Spiniferites validus
									Spiniferites sagittarius
									Spiniferites tihanyensis
									Romanodinium areolatum
									Nematosphaeropsis bicorporis
									Spiniferites 75. form
									Dinoflagellata 139. form
									Dinoflagellata 28. form
									Tectatodinium pellitum
									Botryococcus braunii
									Spirogyra 1. type
									Spirogyra 2. type
									Spirogyra 3c. type
									Cooksonella circularis
									Pediastrum simplex
									Pediastrum boryanum
									Mougeotia laetevirens
									Tetraedron cf. minimum
									Micrhystridium sp.
									Closterium kützingii
									Mougeotia 3. type
									Zygnema sp.

SIGNS: ----- a few specimens
 ————— medium
 ————— frequent

Vertical distribution of organic skeleton microplankton remnants, by ideal interpretation of their frequency within the zones

According to JÁMBOR et al. (1985) the Pannonian s.l. stratum complex means a sedimentation complex formed some time between 2 and 12 million years ago. This stratum complex is divided into eight zones; the dinoflagellate zones are within two main zones (Table 1). For the typical locations of the zones the lithofacies is given according to JÁMBOR (1980, 1985), or after his personal information. (The geographical situation of the locations is shown in Fig. 2).

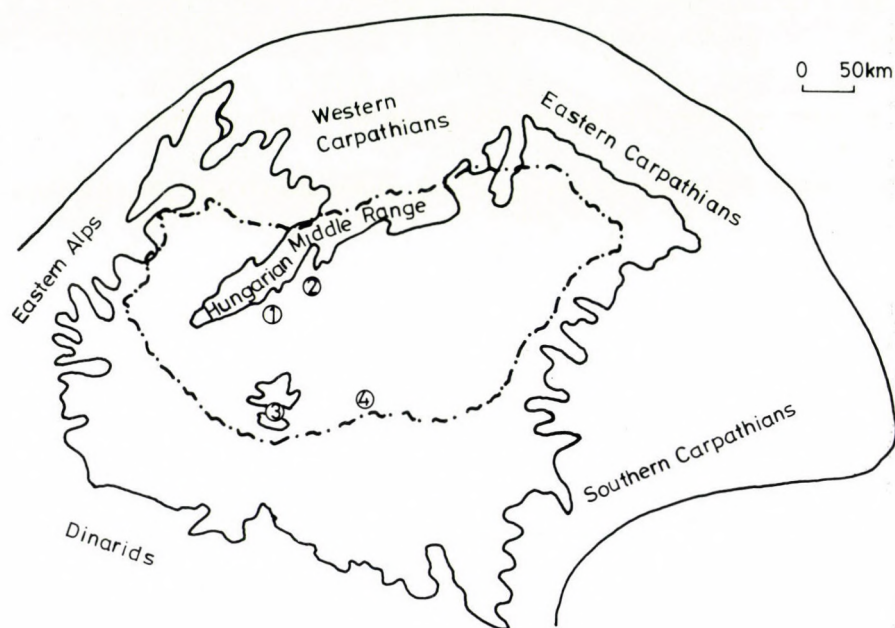


Fig. 2. Distribution of Pannonian formations within the Carpathian basin, after BALÁZS E. et al. 1981, with the type localities of microplankton zones. 1. Lajoskomárom, 2. Pusztazámor, 3. Máriakéménd; Nagykozár, 4. Bácsalmás

LOWER PANNONIAN STAGE

Mecsekia ultima zone

Typical locality: Lajoskomárom-No. 1 bore-hole 663.0–668.2 m, Zala Marl Formation; Further localities: Tengelice-No. 2 bore-hole 663.9–665.0 m; Tengelice No. 1 bore-hole 666.5–667.6 m; Budajenő-No.2 bore-log 198.0–216.0 m;

Pusztazámor-No. 2 bore-hole 79.0-79.2 m; Szirák-No. 2/a bore-hole 724.1-763.4 m; Nagykozár-No. 2 bore-hole 289.15-291.5 m; Association of the zone:

Mecsekia ultima (Sütő-Szentai 1982) comb. nova, Pachysphaera pelagica Ostenfeld, Lingulodinium machaerophorum (Defl. et Cooks.) Wall, Polysphaeridium zoharyi (Ross.) Bujak et al., Mecsekia orientalis sp. nova, Hidasia sp., Cymatiosphaera sp. indet., Lingulodinium varium Sütő-Szentai, Spiniferites cf. bentori (Rossignol), Mecsekia incrassata Sütő-Szentai, Mecsekia spinosa Hajós, Spirogyra type l. B. Van Geel et al., Botryococcus braunii Kützing, Foraminifera (organic).

The development of the species from the upper Sarmatian Mecsekia associations can be best studied in the Lajoskomárom-No. 1 bore-hole.

The first appearance of the species is still accompanied by many Sarmatian elements, which is followed by its dominant occurrence. The species in its dominance level is here and there autocratic, accompanied only by some cosmopolitan elements (Botryococcus, Spirogyra), in other places it is accompanied by Sarmatian elements, though their frequency shows an upward decreasing tendency.

Spiniferites bentori main zone

The main zone is characterized by the mass occurrence of Spiniferites bentori-Gonyaulax digitale type Dinoflagellatae.

The ecological conditions of the Pannonian inland sea were favourable for the reproduction of these Dinoflagellatae. The fact that the environment is optimum for the species is indicated besides its mass occurrence by the large number of variational forms. In this morphologically rich, diversified community three major development stages of the species can be distinguished within the main zone.

The lower stage is characterized by the bentonic and planktonic dimorphous forms of the species, from the primitive forms to the developed and morphologically highly diversified - roundish and pear-shaped - variation. The oval, elongate bentonic elements, the intermediate and pontiadinoid forms appear in the second stage. In the third stage the pontiadinoid character is dominant, or in some places autocratic.

Spiniferites bentori pannonicus zone

Type localities: Pusztazámor-No. 2 bore-hole 74.0-79.0 m Csákvár Formation; Further occurrences: Lajoskomárom-No. 1 bore-hole 663.0-592.0 m

(Zsámbéki F., Beleznai Formation); Som-No. 2 bore-hole 493.8–496.4 m; Buda-jenő-No. 2 bore-hole 96.3–198.0 m; Szirák-No. 2 bore-hole 549.3–564.7 m; Szirák-No. 2/a bore-hole 559.4–696.7 m; Detk-No. 1 bore-hole 731.4–756.6 m; Bóly-No. 1 bore-hole 476.5–481.6 m; Nagykozár-No. 2 bore-hole 264.9–286.25 m.

Community characteristic of the zone:

Spiniferites bentori (Rossignol) Wall et Dale subsp. pannonicus Sütő-Szentai

Spiniferites bentori (Rossignol) Wall et Dale subsp. granulatus subsp. nova

Spiniferites bentori (Rossignol) Wall et Dale subsp. bentori comb. nova

Spiniferites bentori (Rossignol) Wall et Dale subsp. mátraensis subsp. nova

Spiniferites bentori (Rossignol) Wall et Dale subsp. piriformis subsp. nova

Spiniferites bentori var. truncata (Rossignol) Wall et Dale

Spiniferites cf. bentori (Rossignol)

Spiniferites ramosus (Ehrenberg) Serjeant

Spiniferites sp. (membranous forms)

Gonyaulax digitale (Pouchet) Kofoed subsp. primus subsp. nova

Gonyaulax digitale (Pouchet) Kofoed subsp. secundus subsp. nova

Gonyaulax digitale (Pouchet) Kofoed subsp. tertius subsp. nova

Dinoflagellata 70, 71, 72 forms

Hystrichosphaeridae (other, unidentified forms)

Cymatiosphaera sp. indet. (coming from the Sarmatian)

Mecsekia incrassata Sütő-Szentai (coming from the Sarmatian)

Hidasia sp. (coming from the Sarmatian)

Foraminifera (organic walled) (coming from the Sarmatian) Cosmopolitan elements:

Botryococcus braunii Kützing

Spirogyra type 1. B. Van Geel et T. Van Der Hammen

Spirogyra type 2. B. Van Geel et T. Van Der Hammen

Spirogyra type 3c. B. Van Geel et T. Van Der Hammen

Cooksonella circularis Nagy

Pediastrum boryanum Menegh

Pediastrum simplex Meyen

In the Pusztázámor-No. 2 bore-hole the zone community was studied on the basis of 45 samples. In this community only the bentonic dimorphous form occurred; in the 5 m thick stratum complex the morphological changes of the species are easy to follow vertically. The first specimens – in the first association of the species – are thin-walled, almost smooth and greenish white to light yellow in colour (when 1000x magnified). Their appendages are short, the threefold articulation at the ends is little dif-

ferentiated. The apical horn is visible but not yet elongated. They are roundish or slightly ovoid in shape. In its second association the species is characterized by a thicker wall; they are golden yellow in colour, finely granular, and diversified in shape, from roundish to pear-shaped. Their appendages are shorter or longer, the threefold division at the ends is better seen.

In the third association of the species the specimens are golden — to dark yellow, have thicker, roughly granulated walls and diversified — roundish to pyriform — shapes. Beside smaller specimens, 50–60 μm in diameter, larger ones of 80–85 μm diameter are also found. Membranous forms are also characteristic here.

In several bore logs it is characteristic of the lower part of the zone that it starts with bentonic elements alone — though this may be a function of the facies. In the Lajoskomárom-No. 1 bore-hole e.g. in the Zsámbék Marl only bentonic elements were found (at 662–663 m), while in the following Belezna Formation the planktonic dimorphous forms of the species appear between 662 and 592 m.

The benthic and planktonic dimorphous forms can be identified even in the case of a fossile species, on the basis of the shape and size of the plankton body, position of appendages and/or tabulae, shape of the archeopyle. The occasionally different dominance of the planktonic and benthic forms suggests that their habitats were bound to different facies. The Spiniferites bentori pannonicus is a benthic element, its planktonic dimorphous form is the Gonyaulax digitale primus and the 72 forms; the dimorphous form of the Spiniferites bentori granulatus is the Gonyaulax digitale secundus; while the Gonyaulax digitale tertius form may be that of the Spiniferites bentori bentori.

Spiniferites bentori oblongus zone

Type locality: Máriakéménd-No. 3 bore-hole 64.0–73.8 m (south of the Mecsek mountain) Csákvári F., Zalai F., within Tinnye Formations. Further occurrences: Lajoskomárom-No. 1 bore-hole 559.4–592.0 m; Som-No. 1 bore-hole 472.0–488.1 m; Szőlád-No. I/1 bore-hole 219–227.5 m; Zalaszentlászló-No. 1 bore-hole 236.1–251.6 m; Budajenő-No. 2 bore-hole 70.0–96.3 m; Szirák-No. 2 bore-hole 383.0–434.4 m; Detk-No. I bore-hole 682.0–728.7 m; Kaskantyú-No. 2 bore-hole 1154.4–1162.1 m; Bácsalmás-No. 1 bore-hole 528.1–529.8m; Nagyközár-No. 2 bore-hole 227.0–256.7 m; Bóly-No. 1 bore-hole 448.5–476.5 m;

Beside elements coming over from the lower zone new species in the association of the zone are:

Spiniferites bentori (Rossignol) Wall et Dale subsp. oblongus Sütő-Szentai
Spiniferites sp.

Spiniferites nodosus (Wall 1967) Sarjeant 1970

Nematosphaeropsis balcombiana (Deflandre et Cookson) Williams et Downie

Chytroeisphaeridia cariacensis Wall

Chytroeisphaeridia hungarica Sütő-Szentai

Dinoflagellata 129.220 forms

Millioudodinium lörentheyi sp. nova

Gonyaulax digitale (Pouchet) Kofoid subsp. quatuor subsp. nova

Gonyaulax digitale (Pouchet) Kofoid (pontiadinioid form)

Pontiadinium pécsváradensis Sütő-Szentai

Pontiadinium obesum Sütő-Szentai

Millioudodinium baltesi Sütő-Szentai

Cosmopolitan elements:

Cooksonella circularis Nagy

Botryococcus braunii Kützing

Spirogyra type 1. B. Van Geel et al.

Spirogyra type 3c B. Van Geel et al.

Mougeotia laetevirens (A. Braun) Wittrock

The association of the zone is the richest of all within the Spiniferites bentori main zone, concerning the morphological variations and the frequency of Dinoflagellatae.

Of the species Spiniferites bentori-Gonyaulax digitale only two dimorphous forms occurred in the former zone; in this zone further two morphological variations or intermediate prevolvate stage forms are found: one of them is the Chytroeisphaeridia cariacensis, which has neither appendages nor tabulae but as for its order of magnitude, on the basis of the archeopyle it is identical with the species; the other is the Chytroeisphaeridia hungarica, which occasionally is similar in size to, though sometimes much smaller than the C. cariacensis, and the archeopyle is compound, not the 3" table. The latter is the simplest stage, it can be followed to the last limit of occurrence of Dinoflagellatae (Fig. 3a-e).

A new morphological phenomenon is the pontiadinioid theca, that is the development of the antapical horn; and the appearance of a few specimens of species from the Pontiadinium genus. In the Dinoflagellatae association even the size of dimorphous specimens of the same species or subspecies is varied,

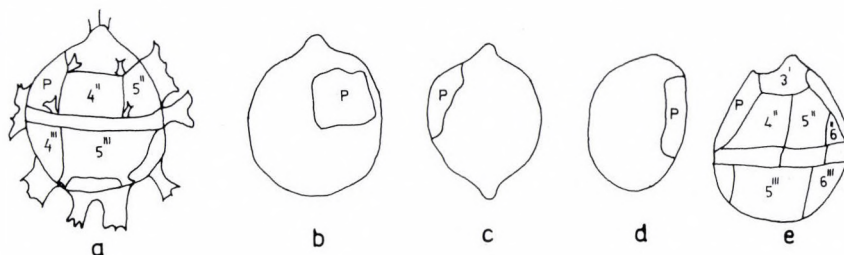


Fig. 3. Some characteristic elements of the microplankton zones. a: Spiniferites bentori (benthic element); b-d: intermediate stage, b=129. form; c=220. form, d=Chytroeisphaeridia caricoensis; e: Gonyaulax digitale (planktonic element)

ranging between 50 and 80 micrometre. The benthic elements are deeply lobed though maintaining the threefold division. The oval, oblong benthic forms are characteristic (Spiniferites bentori oblongus).

Pontiadinium pécsváradensis zone

Type locality: Lajoskomárom-No. 1 bore-hole 519.4–533.5 m Zámor Formation; Further localities: Som-No. 1 bore-hole 457.0–472.0 m; Zalaszentlászló-No. 1 bore-hole 226.6–235.1 m; Máriakéménd-No. 3 bore-hole 50.0–55.0 m; Egerág-No. 7 bore-hole 348.5–348.8 m; Nagykozár-No. 2 bore-hole 212.0–227.0 m; Bácsalmás-No. 1 bore-hole 523.9–528.1 m; Kaskantyú-No. 2 bore-hole 1144.6–1144.9 m; Szirák-No. 2 bore-hole 373.0–383.0 m; Detk-No. I bore-hole 667.2–682.0 m; Fertőrákos-No. 21 bore-hole 31.0–37.0 m;

The association of the zone was studied most circumstantially in the Bácsalmás-No. 1 bore-hole, from 21 samples of a 4.2 m thick stratum. The association was easy to identify in all bore-holes. Where these planktonic elements are dominant, the associations are strikingly similar irrespective of the geographic situation. Among the planktonic forms the large pontiadiniums are the most characteristic. Benthic elements seldom occur in the association.

The association of the zone:

Pontiadinium inequicorutum (Baltes) Stover et Evitt

Pontiadinium obesum Sütő-Szentai

Transitional forms of Pontiadinium obesum-pécsváradensis-inequicorutum species

Gonyaulax digitale (Pouchet) Kofoid subsp. tertius subsp. nova

Gonyaulax digitale (Pouchet) Kofoid subsp. primus subsp. nova

Millioudodinium lörentheyi sp. nova

Nematosphaeropsis balcombiana (Defl. et Cookson) Williams et Downie

Spiniferites sp.

Elements of Spiniferites bentori (Rossignol) subspecies coming over from the lower zone.

Spiniferites sp. (membranous forms)

Spiniferites ramosus (Ehrenberg) Sarjeant

Chytroeisphaeridis cariacensis Wall

Chytroeisphaeridis hungarica Sütő-Szentai

Dinoflagellata 129. 220. forms and their oblong variations

Dinoflagellata 70., 71. and 72. form

Millioudodinium baltesi Sütő-Szentai

Cosmopolitan elements:

Spirogyra type 1. B. Van Geel et al.

Spirogyra type 3c. B. Van Geel et al.

Mougeotia laetevirens (A. Braun) Wittrock Upper Pannonian substage

Spiniferites balcanica main zone

It is divided into two zones, the lower Spiniferites bentori coniunctus -S. paradoxus-, and the upper Spiniferites validus zone.

Spiniferites balcanica (Thalassiphora balcanica Baltes 1971), a species appearing on the lower border of the main zone, with its different morphological variations characterizes the two zones. It was observed to occur outside the stratum complex rich in Dinoflagellatae.

Spiniferites bentori coniunctus-S. paradoxus zone

Type locality: Nagykozár-No. 2 bore-hole 212.0-147.0 m; within the Csákvár Formation; Further occurrences: Máriakéménd-No. 3 bore-hole 21-50.0 m; Pécsvárad-15 No. T-22 bore-hole 57.6-63.0 m; Egerág-No. 7 bore-hole 297.6-297.9 m; Szentlőrinc-No. XII bore-hole 450.6-516.0 m; Igal-No. 7 bore-hole 634.4-638.4 m; Paks-No. 2 bore-hole 603.0-627.3 m; Tengelic-No. 2 bore-hole 620.0-640.7 m; Tengelic-No. 1 bore-hole 630.0 m; Lajoskomárom-No. 1 bore-hole 472.5-517.2 m; Som-No. 1 bore-hole 388.3-457.0 m; Szőlád-No. I 190-209.8 m; Inota-No. 87 bore-hole 55-67.1 m; Zalaszentlászló-No. 1 bore-hole 197.8-219.5 m; Ukk-No. 3 bore-hole 180-190.5 m; Bácsalmás-No. 1 bore-hole 488-523.9 m; Kaskantyú-No. 2 bore-hole 1090.0-1142.7 m; Szirák-No. 2

bore-hole 272.95–294.3 m; Detk-No. I bore-hole 547–657 m; Kun-No. 1 bore-hole 2557–2560 m; Kun-No. 2 bore-hole 2592–2597 m; Farnos-No. 5 bore-hole 1308–1311 m; Jászberény Ny-No. 1–9. bore-hole 1507–1509 m;

Association characteristic of the zone:

Spiniferites bentori (Ross.) Wall et Dale subsp. coniunctus Sütő-Szentai

Spiniferites bentori (Ross.) Wall et Dale subsp. oblongus Sütő-Szentai

Spiniferites bentori (Ross.) Wall et Dale subsp. bentori comb. nova

Nematosphaeropsis balcombiana (Defl. et Cookson) Williams et Downie

Spiniferites balcanica (Baltes 1971) comb. nova

Spiniferites paradoxus (Cookson et Eisenach) Sarjeant

Spiniferites sp.

Spiniferites ramosus (Ehrenberg) Sarjeant

Spiniferites tengelicensis Sütő-Szentai

Spiniferites nodosus (Wall) Sarjeant

Spiniferites sp. (membranous forms)

Millioudodinium detkensis Sütő-Szentai

Millioudodinium foveolatum Sütő-Szentai

Millioudodinium balteri Sütő-Szentai

Millioudodinium pelagicum Sütő-Szentai

Millioudodinium jámbori sp. nova

Millioudodinium transdanuvianum Sütő-Szentai

Millioudodinium quadratum sp. nova

Gonyaulax digitale (Pouchet) Kofoid subsp. quatuor subsp. nova

Gonyaulax digitale (Pouchet) Kofoid subsp. tertius subsp. nova

Impagidinium globosum Sütő-Szentai

Impagidinium spongianum Sütő-Szentai

Impagidinium cf. globosum Sütő-Szentai

Gonyaulax pannonicus Nagy

Pontiadinium pécsváradensis Sütő-Szentai

Chytroeisphaeridia tuberosa Sütő-Szentai

Chytroeisphaeridia cariacensis Wall

Chytroeisphaeridia hungarica Sütő-Szentai

Tectatodinium pellitum Wall

Dinoflagellata 129., 220. forms (intermediate stages)

Dinoflagellata planktonic thecae:

forms 29, 38, 66, 67, 70, 71, 72, 74, 119, 201, 202, 205, 215, 226, 227, 219.

Cosmopolitan elements:

Botryococcus braunii KützingSpirogyra type l. B. Van Geel et al.Mougeotia laetevirens (A. Braun) WittrockTetraedron cf. minimum HansgirgCooksonella circularis Nagy

In the association beside the lower Pannonian transit forms the new morphological variations of Dinoflagellatae indicate the change of environment: the species Spiniferites paradoxus, S. balcanica, S. tengelicensis, Millioudodinium detkensis, that is, those membranous Dinoflagellatae which do not occur in the lower zones. Further, the subspecies Spiniferites bentori coniunctus and its variations, transitional (benthic) forms between the species Spiniferites bentori and Spiniferites validus are characteristic of the association. In the bore logs examined the benthic elements are concomitants of the planktonic thecal association, their frequency does not even come close to the frequency of benthic elements in the lower Pannonian zones. Among the planktonic thecae I. globosum, G. pannonicus, I. spongianum, M. foveolatum, M. pelagicum, M. jámbori are frequent.

In the zone the masses of planktonic elements and the Spiniferites balcanica type membranous dinoflagellatae may be basin associations of transgression character.

Spiniferites validus zone

Type locality: Bácsalmás-No. 1 bore-hole 313.6–468.0 m (in the southern part of the Danube-Tisza Interfluve) Nagykörű Formation; Further localities: Som-No. 1 bore-hole 183.1–386.7 m; Lajoskomárom-No. 1 bore-hole 396.7–428.6 m; Tengelic-No. 1 bore-hole 601–603.0 m; Tengelic-No. 2 bore-hole 564.0–614.0 m; Paks-No. 2 bore-hole 573.8–578.8 m; Igal-No. 7 bore-hole 329.5–628.1 m; Gálosfa-No. 1 bore-hole 192.3–311.4 m; Szentlőrinc-No. XII bore-hole 104.5–450.6 m; Bóly-No. 1 bore-hole 177.0–353.0 m; Nagykozár-No. 2 bore-hole 376.0–1080.0 m; Szirák-No. 2 bore-hole 161.3–251.5 m; Detk-No. I bore-hole 376.0–547.0 m; Farmos-No. 1 bore-hole 1200–1205 m;

Association characteristic of the zone:

Spiniferites validus Sütő-Szentai and variations of the speciesSpiniferites ramosus (Ehrenberg) SarjeantSpiniferites sp. form 75.Spiniferites sagittarius Sütő-SzentaiSpiniferites tihanyensis sp. nova

Spiniferites sp. (other forms)

Nematosphaeropsis bicorporis Sütő-Szentai

Spiniferites bentori (Rossignol) Wall et Dale subsp. oblongus subsp. nova

Spiniferites bentori (Rossignol) Wall et Dale subsp. bentori comb. nova

Spiniferites balcanica (Baltes) comb. nova

Romanodinium areolatum Baltes

Dinoflagellata 28, 29, 36, 66, 67, 77, 139, 213, 217, 122, planktonic thecae

Dinoflagellata 129, 220, forms of intermediate stage

Chytroeisphaeridia cariacensis Wall

Chytroeisphaeridia tuberosa Sütő-Szentai

Chytroeisphaeridia hungarica Sütő-Szentai

Tectatodinium pellitum Wall

Pontiadinium inequicornutum (Baltes) Stover et Evitt

Pontiadinium sp. (other forms)

Millioudodinium foveolatum Sütő-Szentai

Millioudodinium pelagicum Sütő-Szentai

Millioudodinium baltesi Sütő-Szentai

Impagidinium globosum Sütő-Szentai

Impagidinium cf. globosum Sütő-Szentai

Impagidinium spongianum Sütő-Szentai

Gonyaulax digitale (Pouchet) Kofoid subsp. tertius subsp. nova

Gonyaulax pannonicus Nagy

Millioudodinium transdanuvianum Sütő-Szentai

Millioudodinium quadratum sp. nova

Millioudodinium punctatum (Baltes) Stover et Evitt

Millioudodinium bacculatum (Baltes) Stover et Evitt

Cosmopolitan elements:

Botryococcus braunii Kützing

Spirogyra type 1. B. Van Geel et al.

Spirogyra type 3c. B. Van Geel et al.

Dinoflagellata-Zygnemataceae intermediate zone

Within the lower and upper border of the zone the occurrence of Dinoflagellatae is scarce. Those to be found are thick-walled, or thinned undeveloped forms. The specimens within the lower and upper border of the zone are the best accommodating dinoflagellata forms from the association of the upper Pannonian Spiniferites balcanica main zone. Their association

does not always mean a younger community, it may replace the associations of the upper pannonian Dinoflagellata zones in a heteropic facies in which the ecological factors were unfavourable for the Dinoflagellatae. Species found in the intermediate zone:

Tectatodinium pellitum Wall, Chytroeisphaeridia cariacensis Wall, C. hungarica, C. tuberosa, Gonyaulax pannonicus Nagy, I. globosum, II. spongianum, Dinoflagellata form 28, 66, 122, 215, 201.

Cosmopolitan elements:

Botryococcus braunii Kützing

Tetraedron cf. minimum Hansgirg

Pediastrum simplex Meyen

Cooksonella circularis Nagy

Mougeotia laetevirens (A. Braun) Wittrock

Micrhystridium sp.

Spirogyra type 1. B. Van Geel et al. (small forms)

The last occurrence of dinoflagellatae was observed within the Tihany Formation, e.g. in the Tengelic-No. 2 bore-hole, between 117.7 and 120.0 m.

Mougeotia laetevirens zone

The fresh-water alga community of pelitic lake sediments in the upper part of the Pannonian stratum complex is designated with this species which occurs though with varying frequency everywhere in the bore logs examined in Hungary. The species was frequent in the Nagyszékely-, Tab-, Polgárdi bore-holes of Central Transdanubia as well as in the Tiszapalkonya-No. I bore-hole in the Great Hungarian Plain, in the latter place even in the upper part of the Dinoflagellata-Zygnemataceae intermediate zone.

Association of the zone:

Mougeotia laetevirens (A. Braun) Wittrock

Spirogyra type 3c. B. Van Geel et al.

Spirogyra type 1. B. Van Geel et al.

Zygnema sp.

Mougeotia type 3. Van Der Hammen et al.

Closterium kützingii Brébisson

Botryococcus braunii Kützing

Pediastrum simplex Meyen

Cooksonella circularis Nagy

The cosmopolitan elements within the Pannonian stratum complex, the Botryococcus, Cooksonella and Zygnemataceae algae are no markers of age,

the lifetime of these species is long, they were encountered in formations both older and younger than the Pannonian. The frequency of a species is determined by the ecological conditions of the habitats, the temperature, pH, salt content and other less known components.

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REFERENCES

- Baltes, N. (1971a): Tertiary Plant Microfossil Assemblages from the Pannonian Depression (Rumania) and their Palaeoecology. — Rev. Palaeobot. and Palynology **11**: 125–158.
- Baltes, N. (1971b): Pliocene Dinoflagellata and Acritarcha in Romania (in Farinacci, A.) — Proceedings Second Planktonic Conference Rome 1970. Edizioni Tecnoscienza, Rome, V/1: 1–19.
- Hajós, M. (1966): A mecseki miocén diatomaföld rétegek mikroplanktonja. — Das Mikroplankton der Kieselgurschichten im Miozän des Mecsekgebirges. — MÁFI Évi Jel. 1964-ről, 139–171.
- Jámbor, Á. et al. (1985): General Characteristics of Pannonian s.l. deposits in Hungary. — Abstracts. Hungarian Geological Survey. 276–284. figs 1–4.
- Jámbor, Á. (1980): A Dunántúli Középhegység pannóniai képződményei. Pannonian formations of the Transdanubian Central Mountains. — MÁFI Évk. LXII: 1–259.
- Jámbor, Á. et al. (1985): Zentrales Mittleres Donaubecken: Bohrung Lajoskomárom Lk-1, S-Balaton — Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys VII: 204–219.
- Nagy, E. (1965): The Microplankton occurring in the Neogene of the Mecsek Mountains. — Acta Bot. Acad. Sci. Hung. **11**: 197–216.
- Nagy, E. (1966). Investigations into the Neogenic Microplankton of Hungary. — The Palaeobotanist **15**: 38–46.
- Sütőné Szentai, M. (1982): Szervesvázú mikroplankton biozónák a Közép-Dunántúl pannóniai rétegösszletében. (Biozones of organic-skeletal microplanktons in the Pannonian layers of the Middle-Transdanubia.) In Hungarian. — MÁFI Évi Jel. 1980-ról. 309–344.
- Sütőné Szentai, M. (1985): Die Verbreitung organischer Mikroplankton — Vergesellschaftungen in den pannonischen Schichten Ungarns. — Chronostratigraphie und Neostatotypen M₆ Pannonien. 516–525.

- Wall, D. (1965): Modern Hystrichospheres and Dinoflagellate cysts from the Woods Hole Region. — Grana Palynologica 6: 297–314.
- Wall, D., Dale, B. (1968): Modern dinoflagellate cysts and evolution of Peridinales. — Micropaleontology 14: 265–304.
- Wall, D., Dale, B. (1970): Living hystrichosphaerid dinoflagellate spores from Bermuda and Puerto Rico. — Micropaleontology 16: 47–58.

Plate I

- Fig. 1. Lingulodinium machaerophorum (Deflandre et Cookson) Wall — Nagykozár
—No. 2 bore-hole 292.3 m
- Fig. 2. Lingulodinium varium sp. nova — Nagykozár— No. 2 bore-hole 292.8 m
- Fig. 3. Cymatiosphaera sp. — Pusztazámor—No. 2 bore-hole 80.2 m
- Fig. 4. Mecsekia orientalis sp. nova — Pusztazámor—No. 2 bore-hole 80.2 m
- Fig. 5. Mecsekia ultima (Sütő-Szentai 1982) comb. nova — Nagykozár—No. 2
bore-hole 291.5 m
- Fig. 6. Mecsekia incrassata sp. nova — Lajoskomárom—No. 1 bore-hole 672–673 m
- Fig. 7. Hsytrichosphaeropsis obscura Habib — Budajenő—No. 2 bore-hole 224.6–
225.6 m
- Fig. 8. Chytroeisphaeridia sp. — Lajoskomárom—No. 1 bore-hole 675–676 m
- Fig. 9. Spiniferites cf. bentori (Rossignol) Wall et Dale — Nagykozár—No. 2
bore-hole 292.8 m
- Fig. 10. Spiniferites bentori (Rossignol) Wall et Dale subsp. budajenőensis
subsp. nova — Budajenő—No. 2 bore-hole 219 220.1 m

Figs 1–10. 750x

Plate II

- Figs 1–2. Spiniferites bentori (Rossignol) Wall et Dale subsp. pannonicus
subsp. nova — Pusztazámor—No. 2 bore-hole 78.4 78.5 m
- Fig. 3. Spiniferites bentori (Rossignol) Wall et Dale subsp. granulatus
subsp. nova — Pusztazámor—No. 2 bore-hole 75.2 75.3 m
- Fig. 4. Spiniferites bentori (Rossignol) Wall et Dale subsp. oblongus
subsp. novus — Máriakéménd—No. 3 bore-hole 71.2 m
- Fig. 5. Spiniferites bentori (Rossignol) Wall et Dale subsp. coniunctus
subsp. nova — Nagykozár—No. 2 bore-hole 172 177.1 m
- Fig. 6. Spiniferites validus Sütő-Szentai — Nagykozár—No. 2 bore-hole
137–142 m

Figs 1–4. 750x

Figs 5–6. 500x

Plate III

- Fig. 1. Millioudodinium lörentheyi sp. nova — Máriakéménd—No. 3 bore-hole
73.8 m
- Fig. 2. Gonyaulax digitale (Pouchet) Kofoid subsp. primus ssp. nova — Lajos-
komárom—No. 1 bore-hole 559.4–581.6 m
- Fig. 3. Pontiadinium inequicornutum (Baltes) Stover et Evitt — Som—No. 1
bore-hole 457–462 m
- Fig. 4. Gonyaulax digitale (Pouchet) Kofoid subsp. secundus ssp. nova — Som
—No. 1 bore-hole 493.8–495.6 m 2. minta

Fig. 5. *Gonyaulax digitale* (Pouchet) Kofoid subsp. *quatuor* ssp. nova —
Som-No. 1 bore-hole 462–467 m

Fig. 6. *Gonyaulax digitale* (Pouchet) Kofoid subsp. *tertius* ssp. nova —
Máriakéménd-No. 3 bore-hole 71.2 m

Figs 1–6. 750x

Plate IV

Fig. 1. *Spiniferites paradoxus* (Cookson et Eisenack) Sarjeant — Nagykozár—
No. 2 bore-hole 192–197 m

Fig. 2. *Spiniferites balcanica* (Baltes) comb. nova — Bácsalmás— No. 1 bore-
hole 433–438 m

Fig. 3. *Impagidinium spongianum* Sütő-Szentai — Bácsalmás—No. 1 bore-hole
523.1–523.3 m

Fig. 4. *Millioudodinium jámbori* sp. nova — Tengelice—No. 2 bore-hole
635.5–636.8 m

Fig. 5. *Impagidinium globosum* Sütő-Szentai — Szirák—No. 2 bore-hole 185.1–
187.4 m

Figs 1–5. 750x

Plate I

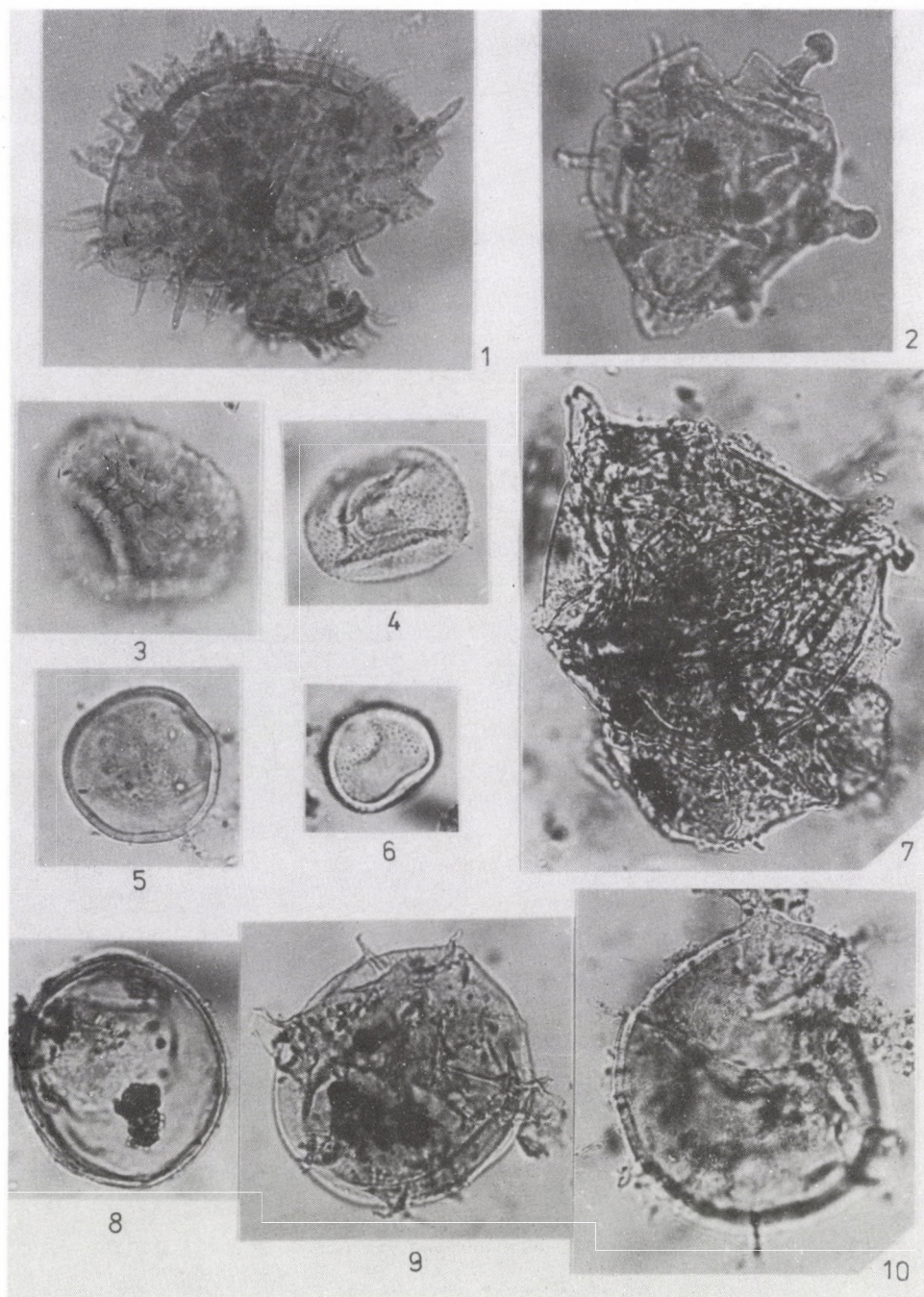


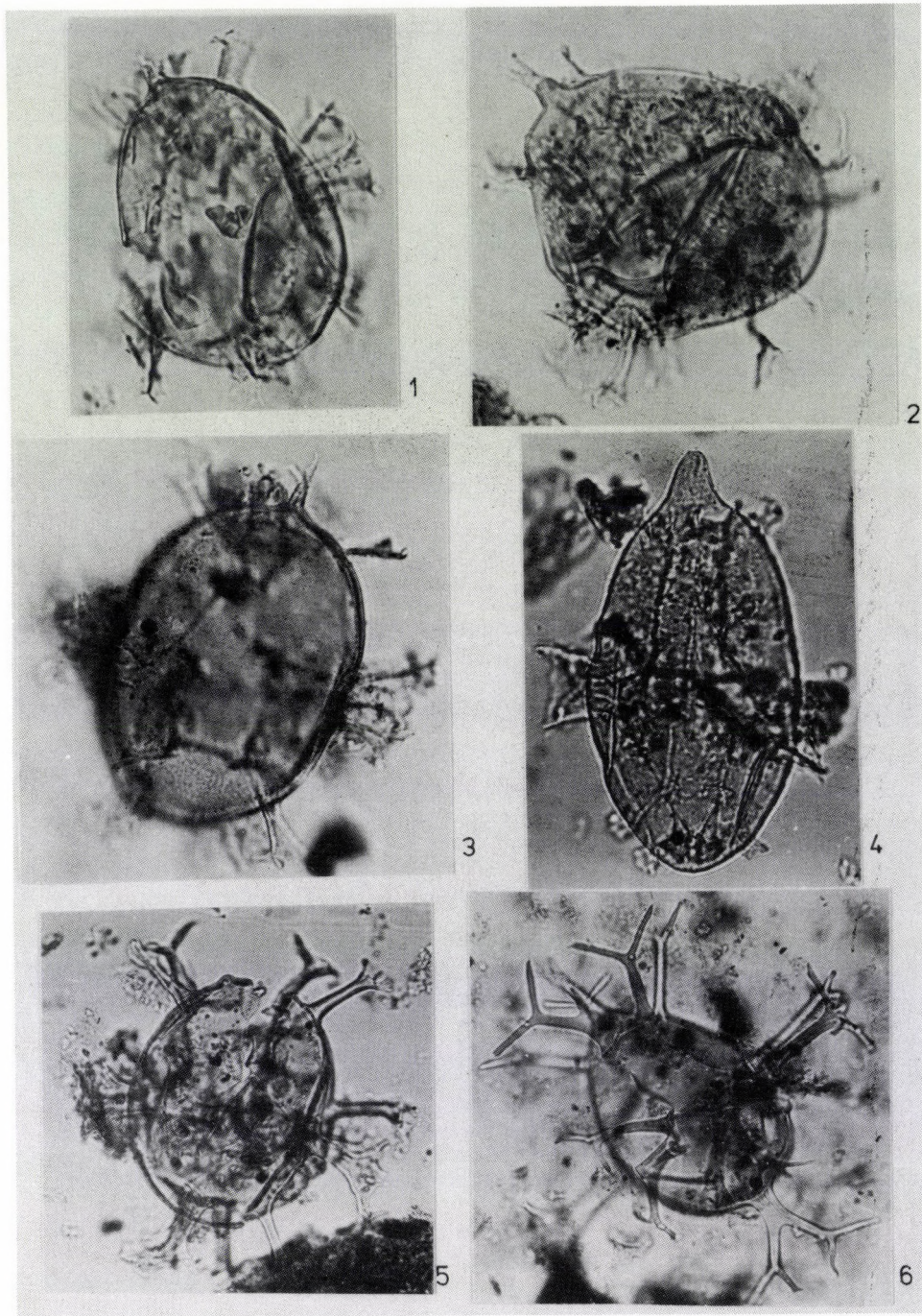
Plate II

Plate III

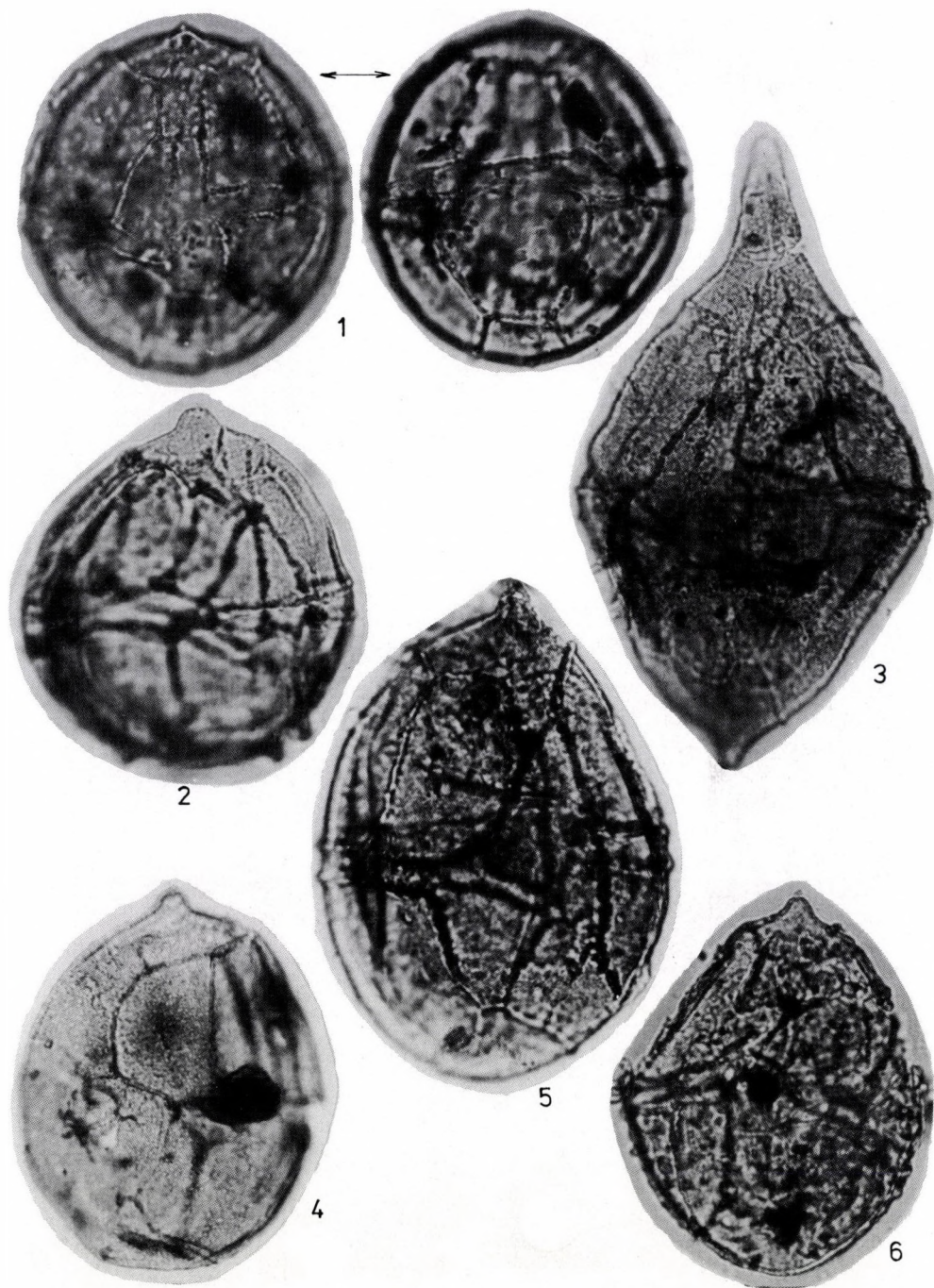
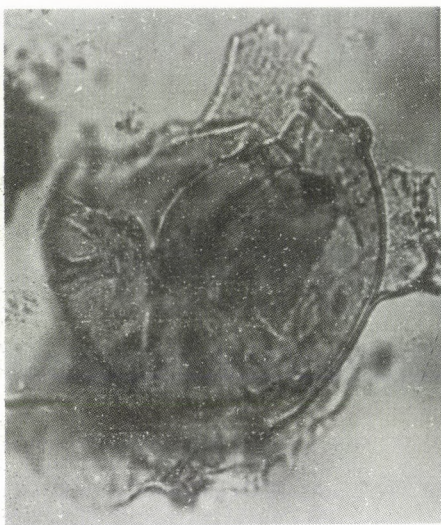
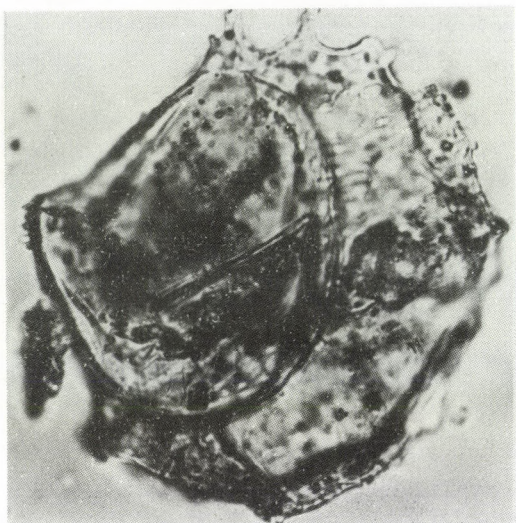


Plate IV

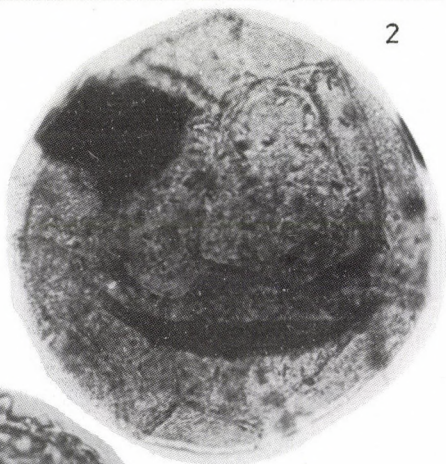
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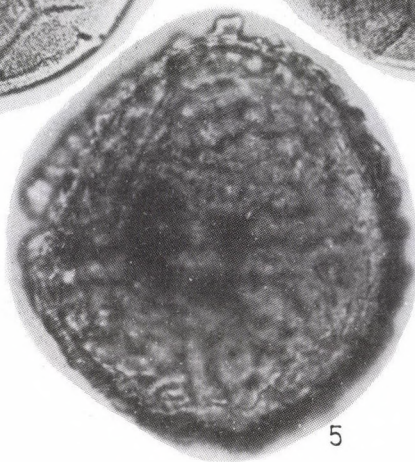
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HIGHER ORGANIZED SPORODERM BIOPOLYMER UNITS OF EQUISETUM ARVENSE L.

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Fresh spores of Equisetum arvense L. were partially degraded with 1-aminoethanol and KMnO_4 solution and investigated by transmission electron microscopy. The basin units of the higher organized biopolymer systems of all three parts of the Equisetum spore (elaters, perispore, exospore) are globular, and arranged in pentagonal polygons.

INTRODUCTION

The biopolymer systems of sporopollenin and its higher organization has been the subject of several publications. Regarding the monomers and the basic biopolymers of the sporopollenin, we cite the publication of TOMSOVIC (1960) and the monograph, edited by BROOKS, GRANT, MUIR, VAN GIJZEL and SHAW (1971). Investigations of the higher organized biopolymer systems of the wall of sporomorphs by indirect methods have been carried out by SITTE (1960) and FREYTAG (1964). The general anisotropic behavior of the sporoderm was emphasized by SITTE (1960), and for the nexine in particular, FREYTAG (1964) using the polarization microscope. FREYTAG suggested that the anisotropic characteristic feature of the nexine probably lies in the organization of short, less solid fibrilles, which may be the fibrillar disposition of globular sporopollenin (?). Other publications have dealt with the direct investigation of the fine structure of recent and fossil spores and pollen grains. AFZELIUS, ERDTMAN and SJÖSTRAND (1954) observed granular - lamellar sporopollenin from spores of Lycopodium clavatum. AFZELIUS (1957), on the basis of TEM investigations of the spore wall of Funaria hygrometrica, established that the single layers of the sporoderm are not amorphous, but possess differences in the electron affinity. This suggests the exine has probably a fibrillar organization. KEDVES, STANLEY and ROJIK (1974) observed globular sporopollenin units on degraded angiosperm exines from the Eocene of Mississippi, USA. ROWLEY and SOUTHWORTH

(1967) observed the deposition of sporopollenin on lamellae of unit membrane dimension. ROWLEY (1967) suggested, that lamellae are often composed of five layers of granules, in other cases the dense wall was composed of about five subunits each approximately 2 μm in diameter. In 1973, ROWLEY commented: "the wall itself is a molecular sieve", later (1975), he suggested; p. 572: "Recent observations (I) indicate that sporopollenin cannot any longer be considered as the only major component of the exine. Filaments in great numbers are exposed from exines of Lycopodium spores heated to high temperatures and sporopollenin is partially dissolved." Concerning the surface of the sporomorphs, ROWLEY (1976) wrote; p. 40: "To be compatible with their environment the surface of microspores must a priori be similar to the surface of tapetal cells. The specific character of a cell's surface is determined by the macromolecules, commonly sugars, and protein, either on or an integral part of the plasma membrane." ROWLEY and PRIJANTO (1977) published a paper on the selective destruction of the exine of pollen grains. In this work the most important concept and methods were described. ROWLEY, DAHL and ROWLEY (1980) published first the helical subunits of the exine, cf. ROWLEY, 1981, ROWLEY, DAHL and ROWLEY 1981, ROWLEY, DAHL, SENGUPTA and ROWLEY 1981. SOUTHWORTH (1985a, b, 1986a, b) established, that after treatment with 2-aminoethanol the exine change to a lattice-like structure of interconnected granules. HESSE (1985) described the outermost region of both the pollen exine and on orbicules in Calluna vulgaris (Ericaceae) isomorphous, identical hemispheres which are 70–80 μm in diameter. KEDVES (1986a, b, c, d, e) published globular sporopollenin units from recent and fossil palynomorphs, and later (1987) from degraded endexine of Taxus baccata with a pentagonal polygon structure, similar to a crystalline organization. This structure is unstable. Now, using the so-called solvent method, several experiments were carried out. As a part of this research program we studied the higher organized biopolymer structures of the spores of Equisetum arvense L. The peculiar morphological and anatomical features of the Equisetaceae were established in the early monographs, and in several further papers; cf. HAUKE (1974). Based on the first LM studies, the alate spores were show to possess elaters (MARLOTH, 1913, GREGUSS, 1941, WELMAN, 1970). GREGUSS (1941) emphasized, that without elaters the identification of the spores of the genus Equisetum is difficult. During the acetolysis process, the spores lose their elaters (ERDTMAN, 1954), but the perine is resistant: ERDTMAN et al. (1961), MCANDREWS et al. (1963). The granular surface of the perine was published by WELMAN (1970). Using the TEM method,

SITTE (1963) distinguished two layers on the elaters of *E. arvense*. Following LUGARDON (1969) the exospore is two layered on the basis of differences in the electron affinity. On the basis of the ultra-thin sections, LUGARDON (1969) presumed, that the spores of *Equisetum* are not alete, but probably have an oval shape tetrad scar. KEDVES (1979) observed this peculiar tetrad scar with SEM. NILSSON *et al.* (1977) published very important LM, TEM and SEM data about the spores of *Equisetum arvense*.

Regarding the object of our experiments, the spores of *Equisetum arvense*, we cite the review of HAUKE (1967: 64): "JOYET - LAVEGNE's work (1926, 1927, 1930, 1931) should certainly be reconsidered. He claimed to have observed two kinds of spores that were separable according to oxidation - reduction potential."

The aim of our experiments are as follows: 1. Taking into consideration the peculiar characteristic features of the Equisetaceae, there are no differences in the basic biopolymer structure to that previously described. 2. Do the different parts of the *Equisetum* spore, elaters, perispore, exospore have different biopolymer structures? There are no differences between the spore wall layers as established by previous studies.

MATERIAL AND METHODS

The sporangia of fertile sprout of *Equisetum arvense* L. were collected by the senior author on the 18th of April 1987. Locality: The left bank of the Tisza River at Újszeged, near the discharge of the Maros into the Tisza. Two kinds of experiments were carried out within the research program of the experimental study of the more highly organized biopolymer units of the plant cell wall; no. 73 and 74. Experiment no. 73: 20 mg fresh spores of *Equisetum arvense* L. + 1 ml 2-aminoethanol, temperature 30°C, length of time 24 h, washing with distilled water until neutral after oxidizing the spores with 10 ml 1% KMnO_4 , temperature 30°C, length of time 24 h. The experiment no. 74 differs from the above mentioned by the length of time of oxidation (48 h). After washing the spores were postfixed with OsO_4 solution, and embedded in Araldite (Durcupan, Fluka). Slides were mounted from the spores in Araldite for LM studies. The ultra-thin sections were made on a Porter Blum ultramicrotome at the EM Laboratory of the Biological Centre of the Hungarian Academy of Sciences. The TEM pictures were taken on a TESLA BS-500 instrument, which has a resolution of 6 Å, in the EM Laboratory of the J.A. University.

RESULTS

1. Light microscopy

Three parts of the spores of *Equisetum arvense* L. were investigated in the two experiments; elaters, perispore and exospore. In general, all elaters in the slides were observed in isolation from the spores and partially incomplete. Rarely did they occur in pairs. Modifications after experiment no. 73: The elaters show fine sculpture, which is evident as granules, the size of which may be in the range of orbicules (Plate I, 1). The margins of the elaters are uneven, because of the above mentioned granules, and also, of the ultrastriate sculpture. At the lamellar ends of the elaters, a stronger corrosion was observed in contrast to the so-called filamental parts of the elaters. Alterations after experiment no. 74; Plate I, 2. KMnO_4 is a high oxidizing agent, so we have observed greater alterations of elaters than in experiment no. 73. In both experiments, the perispore was often complete or partially separated from the spore. Based on the investigation of 200 spores per slide the following modifications were observed:

	S p o r e s		
	with perispore	with fragments of perispore	without perispore
Exp. no. 73	35%	23%	42%
Exp. no. 74	25%	13%	66%

It is clear, that by the length of the oxidation with KMnO_4 the degree of the degradation or detachment of the perispore increased.

2. TEM microscopy

2.1 Elaters

Experiment, no. 73: The cross-section of the filamentous part of the elater (Plate I, 3), clearly shows that the outer layer, is strikingly different from the inner, by its stronger electron affinity. On the picture, taken from the inner part of the elater, the fibrillar ultrastructure may be observed as tiny granules. On the longitudinal ultra-thin sections (Plate I, 4) the lamellar fine structure of the outer layer of the elater may be studied in detail. The darker lamellae are composed of pentagonal shaped higher organized biopolymer units of sporopollenin. The inner holes

of these polygons are full of material with strong electron affinity, and thus the dark lines are composed of tiny granules. The inner layer of the elater has a markedly different electron affinity from the outer one, but the basic structure is the same. The boundary between these two layers is distinct. Experiment, no. 74: The lamellar organization of the pentagonal biopolymer units disintegrated (Plate I, 5). As regards the higher organized biopolymer sporopollenin structure, the terminal lamellar parts of the elaters are identical with those discussed previously; Plate II, 1,2.

2.2 Perispore

The very resistant perispore is covered with globular granules, superficially similar to the orbicules, but during our experiments we have observed a lot of compact forms. The higher organized biopolymer units of these globular forms, and those of the perispore, consist of irregular pentagonal polygons after the processing of experiment no. 73 (Plate II, 3, 4, 5). Experiment, no. 74: The higher organized biopolymer system of the sporopollenin of the globular forms, of the perispore, and of the exospore is well shown on Plate III, 1. The basic structure is identical, but there are differences in the electron density, e.g. the perispore, including the superficial globular forms has a stronger electron affinity than that of the exospore. It is worth mentioning the degradation of the biopolymer structure well shown in particular on the perispore (Plate III, 2).

2.3 Exospore

From our experiments the two layers of the exospore are not well shown. Experiment no. 73: The electron affinity of the exospore is lower than that of the perispore. Strong corrosion happened during the experiments (Plate III, 3, 4; Plate, IV, 1). This may be observed in the organization of the pentagonal polygons, and probably the open polygons (Plate IV, 1) may be a consequence of a strong experimental effect. Experiment no. 74: resulted in clear irregular pentagonal polygon systems (Plate IV, 2, 3; Plate V, 1).

2.4 Endospore

In all probability completely destroyed during the experiments (Plate III, 3) the hiatus between the exospore and the cytoplasm remnants is the site of this layer.

DISCUSSION AND CONCLUSIONS

On the basis of our knowledge to date, we can summarize the molecular organization of the sporoderm as follows. (The importance of the previously mentioned publications of BROOKS and SHAW, ROWLEY et al., and SOUTHWORTH must be emphasized).

1. The level of the monomers; caroten, carotenoid-esters, aromatic lignin derivatives, lipopolysaccharides, cations, etc. These compounds may not be studied with the TEM method.
2. The basic globular biopolymer units forming the primary pentagonal polygons of about 10 Å in diameter.
3. Following SOUTHWORTH (1985a) the single polygons, the globular elements are connected by arms, forming pentagonal polygons.
4. The higher organized pentagonal polygons cf. compound polygons (SOUTHWORTH, 1985a). This biopolymer organization may be regular or irregular. The regular may be lamellar or helical, etc.
5. The open polygons (SOUTHWORTH, 1985a) and the "great globular sub-units" (HESSE, 1985) are at the limit of or less than the resolution of the light microscope.

Regarding the diameter of the primary pentagonal polygons of our present results, in comparison with the previously published data, the most important facts may be summarized as follows:

The largest diameter was observed in the wall of the distinctive algae (*Botryococcus braunii* Kütz.) from the Upper Tertiary oil shale of Hungary (KEDVES, 1986). This result was obtained by experiment no. B.4a.2., with Merkapto-Ethanol only. Further experiments are in progress. It seems that we need to discuss in the future the problems of these methods.

We have recently reviewed the TEM records of the first fossil data from the Eocene of Mississippi (KEDVES et al., 1974). For comparison we show a picture of the degraded exine of *Thomsonipollis magnificus* (Plate V, 2). It is worth mentioning, that the diameters of the single, primary pentagonal polygons of the distinctive early dicotyledonous type *Thomsonipollis* are essentially identical with those of tropical grass pollen type (*Restioniidites*). These primary pentagonal polygons are relatively small.

It is also worth mentioning, that in the case of the exine of *Iaxus baccata* L. the biopolymer system was not open as a result of the experimental studies by the Helix enzyme method (KEDVES 1987a). The solvent method was, however useful in this respect, and a biopolymer system of pentagonal

polygons was discovered on the originally lamellar endexine, the size of these single polygons is 5-6 Å, a little similar to those of the above mentioned two fossil genera.

Regarding our present results on the spores of Equisetum arvense L., the largest pentagonal polygons have been observed on the elaters. The diameter of the pentagonal polygons of the perispore and the exospore are nearly the same.

In conclusion it is necessary to emphasize the following:

1. New experiments are needed to develop our degradations methods.
2. In the future we will try to examine the chemical compounds of the solvents, after the experiments.

ACKNOWLEDGEMENTS

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REFERENCES

- Afzelius, B.M. (1967): On new method in physical cell research and their application in studies of pollen grains and spores. In: ERDTMAN, G. 1957: Pollen and Spore Morphology/Plant Taxonomy. II. Stockholm: 125-134.
- Afzelius, B.M., Erdtman, G., Sjöstrand, F.S. (1954): On the fine structure of the outer part of the spore wall of Lycopodium as revealed by the electron microscope. Svensk Bot. Tidskr. 48: 155-161.
- Brooks, J., Grant, P.R., Muir, M., van Gijzel, P., Shaw, G. (1971): Sporopollenin. Academic Press, London, New York.
- Erdtman, G. (1954): An Introduction to Pollen Analysis. Almqvist and Wiksell, Stockholm.
- Erdtman, G., Berglund, B., Praglowski, J. (1961): An Introduction to a Scandinavian Pollen Flora. Almqvist and Wiksell, Stockholm.
- Freytag, K. (1964): Polarisationsmikroskopische Beobachtungen an Nexinen von Malvaceen-Pollen. Grana Palynologica 5: 277-287.
- Greguss, P. (1941): Die Sporen der mitteleuropäischen Pteridophyten. Mat. és Természettud. Közl. 39: 1-36.
- Gullvag, B.M. (1968): On the fine structure of spores of Equisetum fluviatile var. verticillatum studied in the quiescent, germinated and non-viable state. Grana Palynologica 8: 23-69.

- Hauke, R.L. (1967): Sexuality in a wild population of *Equisetum arvense* gametophytes. Amer. Fern Journ. 57: 59-66.
- Hauke, R.L. (1974): The taxonomy of *Equisetum* - An overview. New Botanist 1: 89-95.
- Hesse, M. (1985): Hemispheric surface processes of exine and orbicules in *Calluna*. Grana 24: 93-98.
- Kedves, M. (1979): Testing of the spores in the *Equisetum* genus. Bot. Közlem. 66: 195-203.
- Kedves, M. (1986a): Dégénération expérimentale de la paroi pollinique. VI Simp. de Paléol. Abstr.: 20.
- Kedves, M. (1986b): Dégénération expérimentale des colonies du genre *Botryococcus* des schistes pétrolifères du Tertiaire supérieur de Hongrie. Acta Biol. Szeged 32: 39-48.
- Kedves, M. (1986c): In vitro destruction of the exine of recent palynomorphs I. Acta Biol. Szeged 32: 49-60.
- Kedves, M. (1986d): Explosion of pollen grains under the electron beam effect of the scanning electron microscope. Acta Biol. Szeged 32: 207-208.
- Kedves, M. (1986e): A complex study of plant microfossils of oil shale by LM, TEM and thin layer chromatography. Bot. Közlem. 73: 25-32.
- Kedves, M. (1987a): In vitro destruction of the exine of recent palynomorphs II. Acta Biol. Szeged 33: in print.
- Kedves, M. (1987b): Higher organized sporopollenin biopolymer structures and the explosion of the pollen grains under scanning effect. Acta Biol. Szeged 33: in print.
- Kedves, M., Stanley, E.A., Rojik, I. (1974): Observations nouvelles sur l'ectexine des pollens fossiles des angiospermes de l'Eocène inférieur. Pollen et Spores 16: 425-437.
- Lugardon, B. (1969): Sur la structure fine des parois sporales d'*Equisetum maximum* Lamk. Pollen et Spores 11: 449-474.
- Marloth, R. (1913): The Flora of South Africa. I.W. Wesley and Son, London.
- McAndrews, J.H., Berti, A.A., Norris, G. (1973): Key to the Quaternary pollen and spores of the Great Lakes Region. Life Sci. Misc. Publ., R. Ont. Mus.: 1-61.
- Nilsson, S., Praglowski, J., Nilsson, L. (1977): Atlas of Airborne Pollen Grains and Spores in Northern Europe. Natur och Kultur, Stockholm.
- Rowley, J.R. (1967): Fibrils, microtubules and lamellae in pollen grains. Rev. Palaeobot. Palynol. 3: 213-226.
- Rowley, J.R. (1973): Translocation through the pollen wall. J. Ultrastruct. Res. 44: 449-450.
- Rowley, J.R. (1975): Lipopolysaccharide embedded within the exine of pollen grains. 33rd. Ann. Proc. Electron Microscopy Soc. Amer.: 572-573.
- Rowley, J.R. (1976): Dynamic changes in pollen wall morphology. The evolutionary significance of the exine, Linnean Society Symposium Series 1: 39-66.

- Rowley, J.R. (1981): Pollen wall characters with emphasis upon applicability. Nordic Journal of Botany 1: 357-380.
- Rowley, J.R., Dahl, A.O., Rowley, J.S. (1980): Coiled construction of exinous units in pollen of Artemisia. 38th Ann. Proc. Electron Microscopy Soc. Amer., San Francisco, California 1980: 252-253.
- Rowley, J.R., Dahl, A.O., Rowley, J.S. (1981): Substructure in exines of Artemisia vulgaris (Asteraceae). Re. Palaeobot., Palynol. 35: 1-38.
- Rowley, J.R., Dahl, A.O., Sengupta, S., Rowley, J.S. (1981): A model of exine substructure based on dissection of pollen and spore exines. Palynology 5: 107-152.
- Rowley, J.R., Prijanto, B. (1977): Selective destruction of the exine of pollen grains. Geophytology 7: 1-23.
- Rowley, J.R., Southworth, D. (1967): Deposition of sporopollenin on lamellae of unit membrane dimension. Nature 213: 703-704.
- Rowley, J.R., Srivastava, S.K. (1986): Fine structure of Classopollis exines. Can. J. Bot. 64: 3059-3074.
- Sitte, P. (1960): Die optische Anisotropie von Sporodermen. Grana Palynologica 5: 289-297.
- Sitte, P. (1963): Bau und Bewegung der Sporen-Hapteren bei Equisetum arvense L. Ber. Naturwiss.-Med.Ver. Innsbruck 53: 193-207.
- Southworth, D. (1985a): Pollen exine substructure. I. Lilium longiflorum. Amer. J. Bot. 72: 1274-1283.
- Southworth, D. (1985b): Pollen exine substructure II. Fagus sylvatica. Grana 24: 161-166.
- Southworth, D. (1986a): Pollen exine substructure. III. Juniperus communis. Can. J. Bot. 64: 983-987.
- Southworth, D. (1986b): Substructural organization of pollen exines. In: Pollen and Spores: Form and Function, Linnean Society of London: 61-69.
- Tomsovic, P. (1960): Bemerkungen zum Feinbau des Sporoderms und seiner Terminologie. Preslia 32: 163-173.
- Welman, W.G. (1970): The South African Fern Spores. South African pollen grains and spores, ed. E.M. Van Zinderen Bakker, sr., VI. A.A. Balkema, Cape Town.

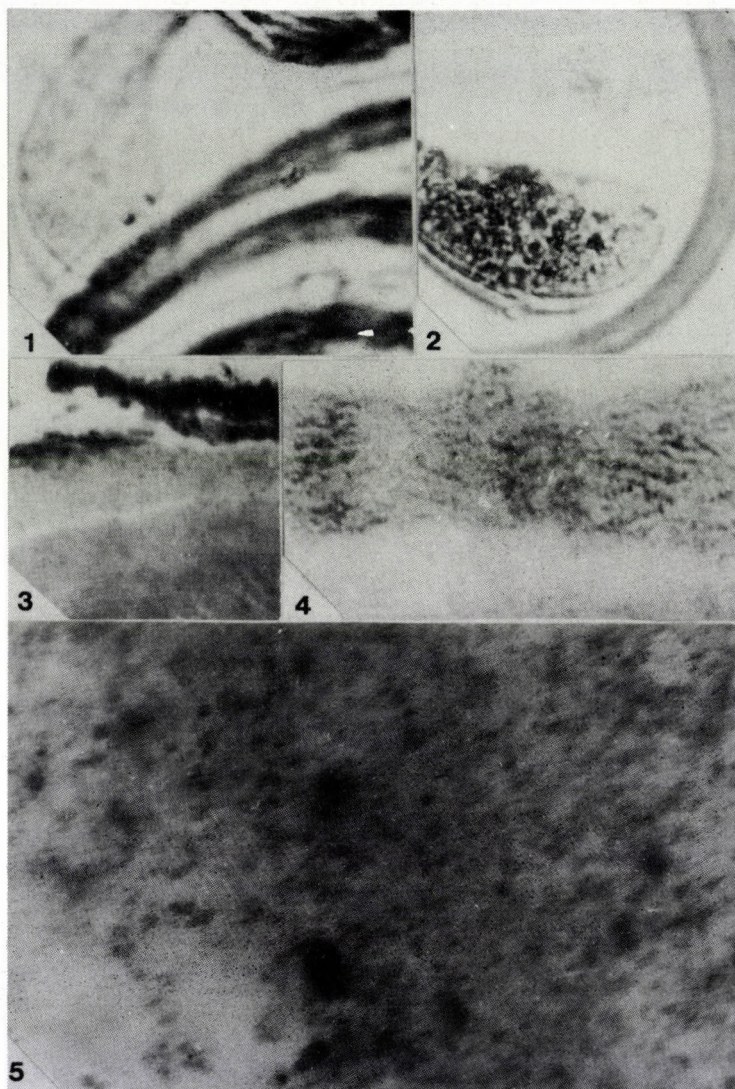


Plate I

Figs 1, 2. LM picture of an elater of *Equisetum arvense* L., 1: experiment no. 73, 2: experiment no. 74, x3000

Fig. 3. TEM picture from the ultra-thin cross-section of an elater; experiment no. 73. The electron affinity of the outer layer is clearly stronger than that of the inner, x50 000

Fig. 4. The higher organized biopolymer units of the outer layer of the elater. Experiment, no. 73, x 250 000

Fig. 5. Higher organized biopolymer units of an elater, experiment no. 74, the disintegration of the pentagonal polygon system is well shown, x200 000

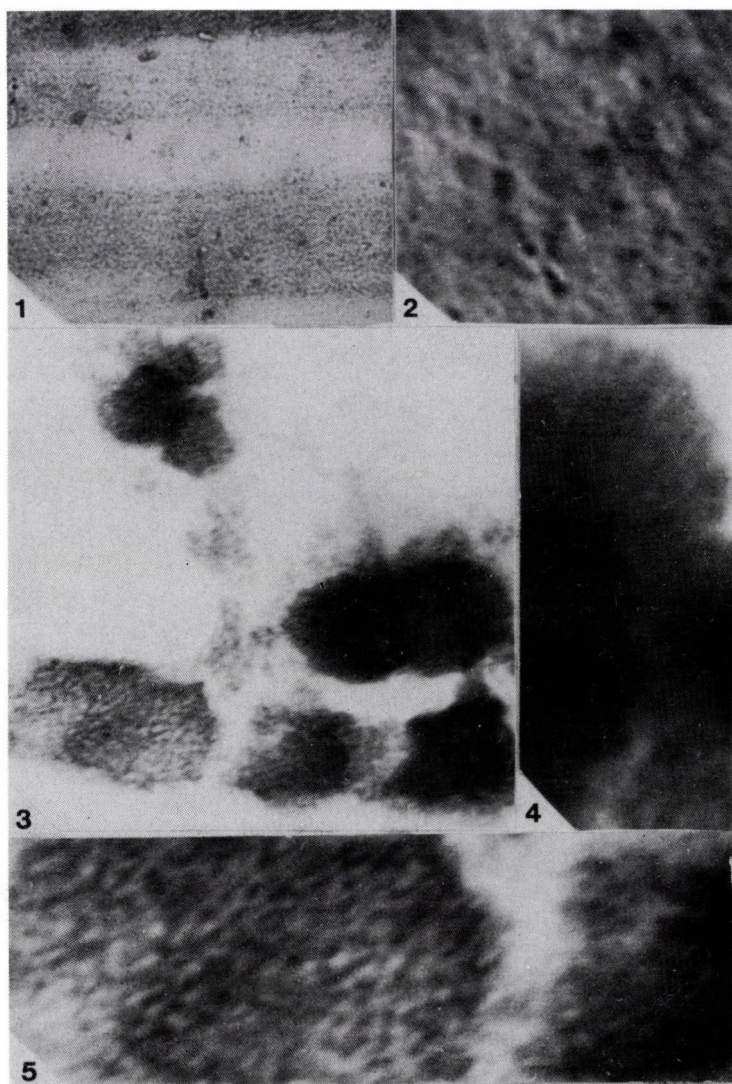


Plate II

- Fig. 1. Ultrastructure and biopolymer organization of the terminal lamellar part of the elater. Experiment no. 73, x100 000
- Fig. 2. Pentagonal polygons from the lamellar part of the elater. Experiment, no. 73, x500 000
- Fig. 3. Higher organized biopolymer units of the perispore and the surficial globular pseudo-orbiculi; experiment no. 73, x200 000
- Fig. 4. Detail from the biopolymer units of the pseudo-orbiculum. Experiment, no. 73, x500 000
- Fig. 5. Detail from the biopolymer units of the perispore. Experiment, no. 73, x500 000

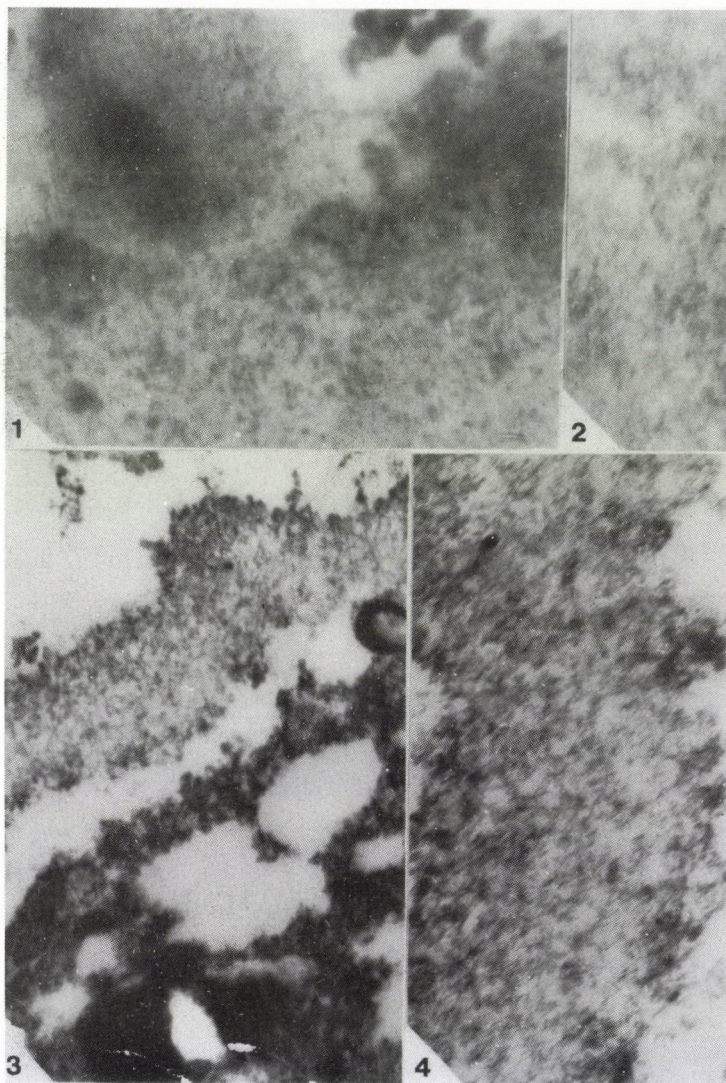


Plate III

Fig. 1. Higher organized biopolymer units of the pseudo-orbiculum, perispore, including outer part of the exospore. Experiment, no. 74, x200 000

Fig. 2. Detail from the partially disintegrated single polygons of the perispore. Experiment no. 74, x200 000

Fig. 3. Exospore, and protoplasm, the endospore is completely degraded. Experiment, no. 73, x50 000

Fig. 4. Detail of the biopolymer system of the exospore. Experiment, no. 73, x100 000

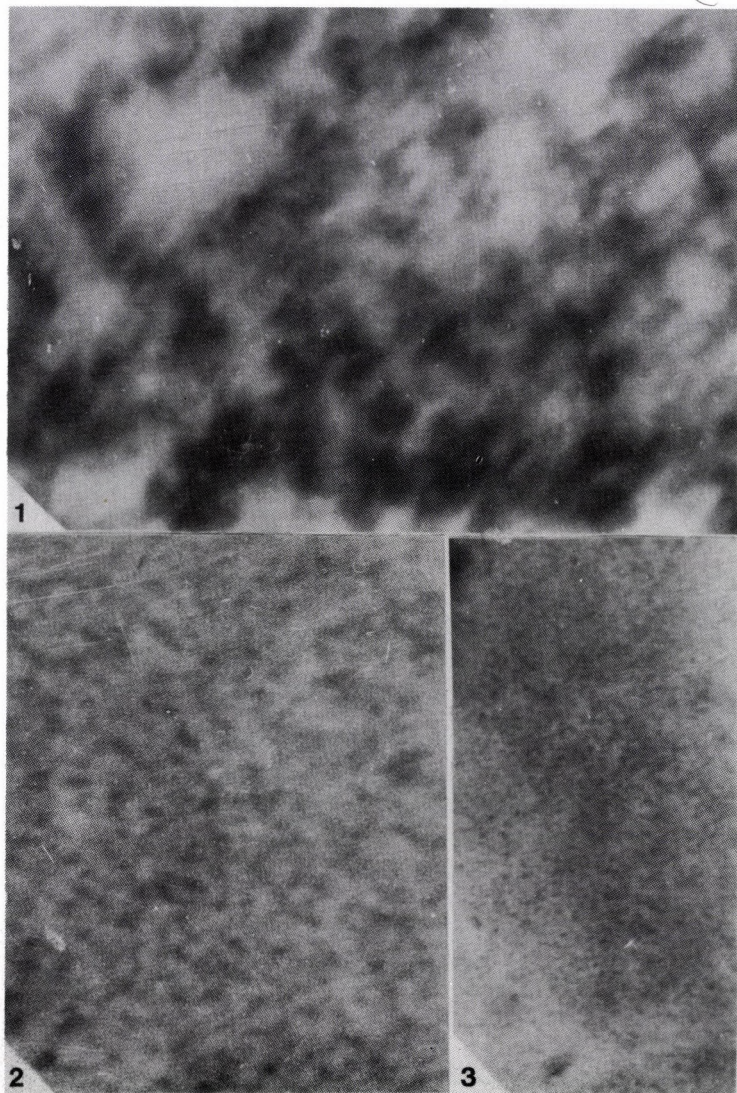


Plate IV

Fig. 1. Detail of the biopolymer units of the exospore. The open polygons are well shown. Experiment no. x500 000

Fig. 2. Detail of the biopolymer system of the exospore. Experiment no. 74, x500 000

Fig. 3. Higher organized biopolymer units, from the exospore. Experiment no. 74, x200 000

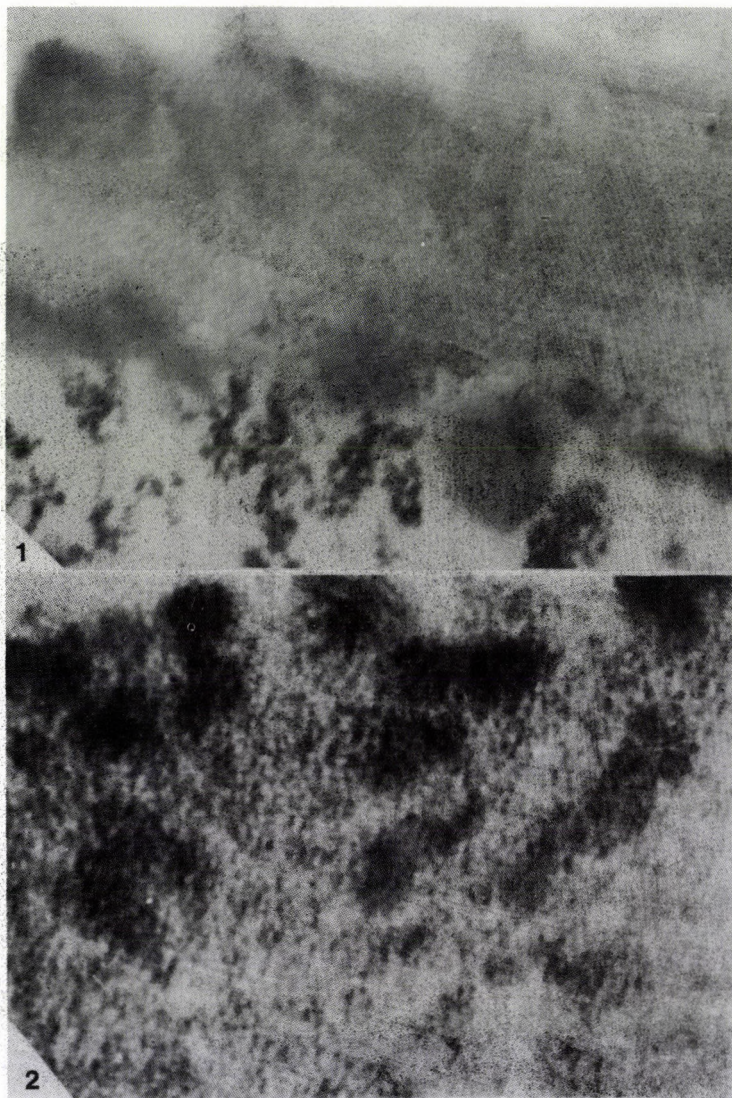


Plate V

Fig. 1. General survey of the exospore. Experiment no. 74. The electron affinity of the inner part is stronger than the outer. x100 000

Fig. 2. *Thomsonipollis magnificus* (Pf. 1953) W. Kr. 1960, exine partially degraded during the taphonomical process of sedimentation. Comparative material from the Eocene of Mississippi U.S.A., detailed study in KEDVES et al. 1974. The small pentagonal polygon biopolymer units are well shown. The higher organized granules are composed of these primary polygons, and of another compound with stronger electron affinity; x500 000

THE RE-CONSIDERATION OF THE GENUS *Cordia* L.

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The genus *Cordia* L. (Boraginaceae) has been re-considered several times from taxonomical point of view. It was splitted into 10 genera by FRIESEN (1933), but at same time it was maintained as an undivided unit by the world monographist of the genus, I.M. JOHNSTON. Palynological studies of several authors suggested a new approach to the taxonomy of this group. More than 100 species of *Cordia* were submitted to a careful study in respect of pollen morphology and calyx structure and floral morphology. Results permit us to suggest the separation of three genera: *Cordia* L., *Varronia* P. Browne and *Gerascanthus* P. Browne and a number of new combinations correlated to these changes.

INTRODUCTION

Cordia L. is a highly variable genus of a pantropical distribution. Its different species were described in the framework of different genera by early classic authors like, PLUMIER, LINNÉ, P. BROWNE, RUIZ et PAVON.

The first review of the genus was made by DE CANDOLLE (1845), who distinguished two genera, *Varronia* DC. non P. BROWNE, including 3 species with calyx opening with circumcised calyptra, and *Cordia* Plum. with 5 sections: *Gerascanthus* Cham., *Rhabdocalyx* A. DC., *Pilicordia* A. DC., *Physoclada* DC. *Sebestenoides* DC., *Myxa* Endl. and *Cordiopsis* A. DC. This concept was followed by GÜRKE in the *Natürlichen Pflanzenfamilien* (1893) with some modifications. In his treatment *Varronia* was included into *Cordia* as a section, and *Cordiopsis* has not been distinguished not even on a section level.

It is BRITTON, who starts dividing *Cordia* into several genera. After the intention of Millspaugh (1909) he also re-establishes *Varronia* of P. BROWNE (1914), than *Sebesten* of DILLENIIUS (1918) and at last describes with MILLSPAUGH (1925) the genus *Calyptracordia*, for distinguishing the species *Cordia alba* (Jacq.) Roem. et Schult. having a calyx opening with calyptra.

Akadémiai Kiadó, Budapest

FRIESEN (1933) went much farther in splitting Cordia and divided it into 10 genera: Myxa Friesen, Collococcus P. Browne, Sebestena Dillen, Calyptracordia Britt. et Wils., Varronia P. Browne em. Friesen, Varroniopsis Friesen, Montjolya Friesen, Ulmarriona Friesen, Gerascanthus P. Browne, and Cordiopsis Desv. em. A. DC. In his cited work FRIESEN has elaborated only one of the ten genera, Varronia, in details.

In opposition to the "ultrarevolutionary" concept of FRIESEN, I.M. JOHNSTON occupied an extremely traditional standpoint by maintaining Cordia as a undividable unit, distinguishing only five sections within the framework of this pantropical genus: Sebestena, Varronia, Gerascanthus, Pilicordia and Myxa.

Just some years later than the last paper of JOHNSTON had appeared (1958) on Cordia, NOWICKE and RIDGWAY (1973) started to study the pollen morphology existing in the Boraginaceae family, including Cordia as well. They established that in the genus Cordia s.l. three different pollen types can be found (1973). MONCADA y HERRERA (1987) studied the pollen grains of 23 Cordia species of the Cuban flora, and they found four morphological types of the pollen grains. Their Type I included some species belonging to the section Sebestena, the Type II included a number of species of the section Varronia, the Type III turned to be common among the species of the sections Gerascanthus and Myxa, and the Type IV was found exclusively in one species: Cordia alba, representing the monotypic genus Calyptracordia Britt. et Wils.

MATERIAL AND METHODS

Field experiences acquired by the first author both in the West Indien and East Africa inspired us to approach the problem from a new direction on a wider geographic and methodological base. Species originated from the Antilles and South America, and a number of African and Asian including some Oceanian taxa have been involved into the study. Besides SEM-micrographs of the pollen grains, floral anatomy with special attention to the opening of calyx, morphology of calyx lobes and to some floral biological features has been studied. More than 170 species were studied, originated partly from own recent collections and types or/and authentic specimens studied in the herbaria B, BP, K, and S.

Type materials of the following species were studied:

Cordia anderssonii Guerke
Cordia axillaris Johnston
Cordia badaeva Urb. et Ekm.
Cordia baracoensis Urb.
Cordia braceliniae Johnst.

Cordia chabrensis Urb. et Ekm.
Cordia claviceps Urb. et Ekm.
Cordia corallicola Urb.
Cordia duartei Borhidi et Muñiz
Cordia exarata Urb.
Cordia ewanii Killip
Cordia fasciculata Urb. et Ekm.
Cordia galapagensis Guerke
Cordia gibberosa Urb. et Ekm.
Cordia guarantiaca Chod. et Hassl.
Cordia iberica Urb.
Cordia jeremiensis Urb. et Ekm.
Cordia lamprophylla Urb.
Cordia llanorum Killip
Cordia lomatoloba Johnst.
Cordia mollissima Killip
Cordia nesophila Johnst.
Cordia opaca Rusby
Cordia paniculata Wikstr.
Cordia paraguariensis Chod. et Hassl.
Cordia petenensis Lundell
Cordia selleana Urb.
Cordia suffruticosa Borhidi
Cordia toaensis Borhidi et Muñiz
Cordia utermarkiana Borhidi

Authentic materials of the following species were studied:

Cordia abyssinica DC.
Cordia acuta Pittier
Cordia alba (Jacq.) Roem. et Schult.
Cordia alliadora (Ruiz et Pav.) Cham.
Cordia anisodonta Urb.
Cordia areolata Urb.
Cordia aspera Fort.
Cordia aurantiaca Baker
Cordia bellonis Urb.
Cordia bicolor A. DC.
Cordia bifurcata Roem. et Schult.
Cordia boissieri A. DC.
Cordia boliviana Gand.
Cordia borinquensis Urb.
Cordia brachycalyx Urb.
Cordia brittonii (Millsp.) Macbr.
Cordia brownei (Friesen) Johnst.
Cordia buchii Urb.
Cordia caffra Sond.
Cordia calcicola Urb.
Cordia chacoensis Chod.
Cordia chamissoniana Steud.
Cordia chaetodonta Melch.
Cordia chrysocarpa Baker
Cordia collococca L.
Cordia colombiana Killip
Cordia cujabensis Cham.
Cordia curassavica (Jacq.) Roem. et Schult.
Cordia dasycephala Desv.

Cordia decandra Hook. et Arn.
Cordia dichotoma Forst.
Cordia diversifolia Pav. ex DC.
Cordia dodecandra DC.
Cordia dwyeri Nowicke
Cordia ecalyculata Vell.
Cordia elliptica Sw.
Cordia ensifolia Urb.
Cordia eriostigma Pittier
Cordia exaltata Lam.
Cordia gerascanthus L.
Cordia gharaf Ehrenb. ex Aschers.
Cordia glabrata A. DC.
Cordia goeldiana Huber
Cordia goetzei Guerke
Cordia grandis Roxb.
Cordia graveolens HBK.
Cordia greggii Torr.
Cordia griffithii C.B. Clarke
Cordia hebeclada Johnst.
Cordia hermanniifolia Cham.
Cordia hypoleuca A. DC.
Cordia ignea Urb. et Ekm.
Cordia inermis Mill.
Cordia insignis Cham.
Cordia kanehirai Hayata
Cordia laevigata Lam.
Cordia lanata HBK.
Cordia latifolia Cham.
Cordia linnaei Stearn
Cordia lucidula Johnst.
Cordia lutea Lam.
Cordia macrantha Chod.
Cordia macrocephala HBK.
Cordia macrostachya (Jacq.) Roem et Schult.
Cordia magnoliifolia Cham.
Cordia megalantha Blake
Cordia microcarpa Killip
Cordia mirabiloides (Jacq.) Roem. et Schult.
Cordia monoica Roxb.
Cordia multispicata Cham.
Cordia myxa L.
Cordia nashii Urb. et Britt.
Cordia nodosa Lam.
Cordia obliqua Willd.
Cordia oblongifolia Thwait.
Cordia panamensis Riley
Cordia panicularis Rudge
Cordia parvifolia A. DC.
Cordia patens HBK.
Cordia paucidentata Fresen
Cordia perroyana Urb. et Ekm.
Cordia picardae Urb.
Cordia platythyrsa Baker
Cordia podocephala Torr.

Cordia poeppigii DC.
Cordia polyantha Benth.
Cordia pringlei Robins.
Cordia rickseckeri Millsp.
Cordia riparia HBK.
Cordia rosei Killip
Cordia rufescens A. DC.
Cordia rupicola Urb.
Cordia salicifolia Cham.
Cordia scaberrima HBK.
Cordia scabrifolia A. DC.
Cordia sebestena L.
Cordia sellowiana Cham.
Cordia sericicalyx A. DC.
Cordia skutchii Johnst.
Cordia sprucei Mez
Cordia superba Cham.
Cordia silvestris auct.
Cordia tetrandra Aubl.
Cordia tortuensis Urb. et Ekm.
Cordia trichoclada A. DC.
Cordia trichotoma Vell.
Cordia verbenacea DC.
Cordia viridis (Rusby) Johnst.

RESULTS

Based on the multilateral studies described above, results permit us to draw the following conclusions. There are three major groups of the species to be distinguished both on floral morphological and palynological evidences at generic level. These are the followings:

Cordia L. em. Borhidi

Cordia L. in Gen. Pl. ed. I. p. 52. 1737. p. p. No. 149. *Sebestena* Dillen. Hort. Eltham., II. p. 340-342. 1732. *Cordia* sect. *Sebestenoides* DC. Prodr. 9:476. 1845.; *Sebesten* Britt. Fl. Berm. p. 309. 1918. *Cordia* sect. *Eucordia* Johnst. Contr. Gray Herb. 92:41. 1930.

Trees and shrubs with terminal corymbose inflorescences, flowers large, showy, corolla tube longer than the calyx, calyx lobes 3-12, corolla lobes 5-16, stamens 5-16, anthers large, oblong, flowers morphologically and physiologically complete, bisexual, fruit large, calyx growing with the mature fruit and becoming fleshy. Pollen grains 3-colpate to 3-colporoidate, sexine reticulate-striate semitectate, colpi long to apocolpium. The striate-reticulate structure more dense around the colpi. Pollen grains loose, easily spreading, pollen kits few or lacking.

The genus is mostly of neotropical distribution including about 20-25 species, most of them from the Caribbean, with one representative in the Palaeotropics. A preliminary list of the species belonging here:

Cordia L. em. Borhidi

Sebestena Dillen. 1732, Adanson 1763; sect. Sebestenoides gen.

Cordia DC. Prodr. 9. 467. 1845., Gürke Nat. Pflanzenfam. Borrag. p. 81. 1893.

Typus generis: Cordia sebestena L.

Cordia angiocarpa A. Rich. in Sagra Hist. Nat. Cub. IX. 1850. p. 110. tab.60.

Cordia boissieri A. DC. in DC. Prodr. 9: 478. 1845.

Cordia brachycalyx Urb. Symb. Ant.

Cordia buchii Urb. Symb. Ant. 1:475. 1900.

Cordia caymanensis Urb. Symb. Ant. 7:344. 1912.

Cordia crispiflora DC. Prodr. 9:476. 1845.

Cordia curbeloi Alain Contr. Ocas. Mus. Hist. Nat. Col. La Salle. 15:9. 1956.

Cordia dodecandra DC. Prodr. 9:478. 1845.

Cordia dumosa Alain Contr. Ocas. Mus. Hist. Nat. 1. c. 59:9. 1956.

Cordia ensifolia Urb. Symb. Ant. 1:476. 1900.

Cordia fitchii Urb. Symb. Ant. 8:576. 1914.

Cordia galeottiana A. Rich. in Sagra Hist. Nat. Cuba IX. 1850. p. 109.

Cordia greggii Torr.

Cordia ignea Urb. et Ekm. Ark. Bot. 22 A No. 17:78. 1928.

Cordia juglandifolia Jacq. Enum. 1760. p. 14.

Cordia leonis (Britt. et Wils.) Ekm. ex Urb. Ark. Bot. 22 A No. 17:77. 1929.

Cordia leucosebestena Griseb. Cat. Plant. Cub. 1866: 208.

Cordia microsebestena Loes. Verh. Bot. Ver. Brand. 55:187. 1913.

Cordia pulverulenta (Urb.) Alain l. c. 15:11. 1956.

Cordia rickseckeri Millsp. Field. Columb. Mus. Bot. 1:522.

Cordia sebestena L. Spec. Pl. I. ed. I. 1753. p. 190.

Cordia subcordata Lam. Illustr. 1889, 1803.

Cordia suckertii Chiovenda, Atti Soc. Nat. Mat. Modena 66:13.

Cordia tortuensis Urb. et Ekm. Erk. Bot. 20 A No.

Cordia triangularis Urb. et Ekm. Ark. Bot. 22 A No. 17:78. 1929.

Varronia P. Browne

Civ. Nat. Hist. Jam. p. 172. tab. 13. f. 2. 1756.; Jacquin Enum. p. 14. 1760.; Desvaux: Varronia J. Bot. 1:257. 1808. non Varronia DC. Prodr. 9:468. 1845.; Varronia Millsp. Praen. Baham. Field. Mus. Bot. 2:311. 1909. Varronia Britton Fl. Virg. Isl. p. 172. 1918. Britton Bull. Torr. Bot. Cl. 50:16. 1914. Britton et Wilson Sci. Surv. Porto Rico and Virg. Isl. New York Acad. 6:122. 1925.; Varronia, Ulmarronia, Varroniopsis et Montjolya Friesen Bull. Soc. Bot. Genève 24:139-143, Cordiopsis Desv. 1808.; Cordiopsis sect. Cordia DC. Prodr. 9:498. 1845. Sect. Myxa Endl. p.p. sensu DC. 1845 and Gürke Borrag. Nat. Pflanzenfam. 83-84. 1893.; Sect. Varronia Johnst. sub Cordia, Contr. Gray Herb. 92:16. 1930.

Shrubs or small trees with terminal or axillary capitate, spicate or very shortly cymose umbellate to globose inflorescences. Flowers (4)-5-merous, mostly small, calyx lobes thickened at the margin, opening regularly, frequently with \pm long appendage. Corolla tube shorter or as long as the calyx, mostly larger than the corolla lobes, often with a hairy ring in the throat. Fruit small, capsule or berry disrupting the calyx while ripening. Pollen grains spheroidal, 3-porate to pantoporate, sexine semitectate, reticulate, heterobrochate with microtubercles on the walls of the reticulum. Pollen loose, easily spread, pollen kitt few or lacking.

Typus generis: Varronia humilis Jacq.

Although the oldest legitimate binomial belonging to this genus is Lantana corymbosa L. (1753), which is cited by BROWNE in his Civil and Natural History of Jamaica, 9. 172. as a synonym of his first species of Varronia, it turns out clearly of his description and figure (t. 13. fig. 2) that his typical species for Varronia is not the Lantana corymbosa of LINNAEUS, but another species described and named later by JACQUIN as Varronia humilis (1760). Even LINNAEUS, when accepted BROWNE's genus Varronia in his Systema Naturae ed. 10. 2:916. 1759, characterized the genus as follows:

VARRONIA. Cal. denticulatis recurvatis. Drupa nucleo 4-loculari

The phrase "Cal. denticulatis recurvatis" refers to the recurved calyx lobes characteristic for Varronia humilis mentioned by BROWNE as having "limbus in quinque lacinias tenuissimas longas reflexas vel intortas divisas" as shown in his figure, as it was explained by STEARN (1971). The selection of the lectotype of the genus must reflect the intention of the original author and therefore I prefer to select Varronia humilis

as typical species of the revalidated genus Varronia, instead of *Lantana corymbosa* L. or Varronia corymbosa (L.) Desv., which does not correspond completely to the generic description of. P. BROWNE.

According to our studies the genus may be divided into four sections:

I. Sectio Varronia

Varronia pro gen. sensu Friesen 1933:139; Sect. *Myxa* subsect. *Dasycephalae* HBK. Nov. Gen. Amer. 3:76. 1818. et in DC. Prodr. 9:496. 1845; et in Gürke Nat. Pflanzenfam. Borrag. 84. 1893. *Varroniopsis* Friesen 1933:142.

Inflorescence capitate or sometimes clavate, calyx lobes with \pm long subulate appendage, corolla lobes shorter than the tube, with hairy ring in the throat.

Type: Varronia humilis Jacq.

II. Sectio Ulmarronia (Friesen) Borhidi comb. nova

Basionym: *Ulmarronia* Friesen Bull. Soc. Bot. Geneve 24:143. 1933; — *Varroniae spicis globosis* HBK; Subsect. *Subcapitatae* DC. sub sect. *Myxa* gen. *Cordia* in Prodr. 9:493. 1845 et in Gürke Nat. Pflanzenfam. Borrag. 84. 1893.

Inflorescence globose, after flowering sub-corymbose, margin of calyx lobes thickened.

Type: Lantana corymbosa L.

III. Sectio Montjolya (Friesen) Borhidi comb. nova

Basionym: *Montjolya* Friesen pro gen. Bull. Soc. Bot. Genève 24:142. 1933. — Syn.: Subsect. *Spiciformes* DC. sub Sect. *Myxa* gen. *Cordia* in Prodr. 9:488. 1845; et in Gürke Nat. Pflanzenfam. Borrag. 84. 1893.

Inflorescence spicate, calyx lobes thickened without a clearly distinguished appendage.

Type: Lantana bullata L.

IV. Sectio Cordiopsis (Desv.) Borhidi comb. nova

Basionym: *Cordiopsis* Desv. in Hamilton Prodr. Fl. Ind. Occ. p. 23. 1825. pro gen.; — Sect. *Cordiopsis* (Desv.) A. DC. sub *Cordia* in DC. Prodr. 9:498. 1945.

Inflorescence short corymbose, calyx lobes with 5 lacinate lobes, corolla hypocrateriform, lobes truncate, obsolete, corrugate in the bud, pollen pantoporate.

Type: Tournefortia serrata L.

The genus with about 150-170 species is essentially of neotropical distribution.

The species belonging to this very well marked and limited genus are cited below with a number of the necessary new combinations.

Varronia sect. Varronia

Varronia acunae Moldenke Phytologia 2:143. 1946. — Cuba

- Syn.: *Cordia acunae* (Mold.) Alain Contr. Ocas. Mus. Hist. Nat. La Salle No. 15:9. 1956.

Varronia anderssonii (Guerke) Borhidi comb. nova — Galapagos

- *Cordia anderssonii* Guerke Nat. Pflanzenfam. Iv. 3:83. 1893.
- Syn.: *Varronia canescens* Andersson Vet. Akad. Handl. Stockholm 1853:203, non HBK.

Varronia areolata (Urb.) Friesen Bull. Soc. Bot. Genève Ser. II. 24:156. 1933. — Hispaniola

- Basionym: *Cordia areolata* Urb. Symb. Ant. 3: 382. 1903.

Varronia asperima (P. DC) Friesen l. c. 155. Prodr. 9:498. 1845. in Urban Symb. Ant. 3:360. 1903.

Varronia asterothrix (Killip) Borhidi comb. nova — Venezuela

- Basionym: *Cordia asterothrix* Killip J. Wash. Acad. Sci. 17:330. 1927.

Varronia axillaris (M. I. Johnst.) Borhidi comb. nova — Brazil

- Basionym: *Cordia axillaris* M. I. Johnston Contr. Gray Herb. n. s. 92:35. 1930.

Varronia badaeva (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia badaeva* Urb. et Ekm. Ark. Bot. 22 A, 17:85. 1929.

Varronia bahamensis (Urb.) Millsp. Field. Mus. Bot. 2:310. 1909.

- Basionym: *Cordia bahamensis* Urb. Symb. Ant. 1:392. 1900.

Varronia baracoënsis (Urb.) Borhidi comb. nova — Cuba

- Basionym: *Cordia baracoënsis* Urb. Ark. Bot. 22 A 17:82. 1929.

Varronia barahonensis (Urb.) Friesen l. c. 172 — Hispaniola

- Basionym: *Cordia barahonensis* Urb. Symb. Ant. 7:345. 1912.

Varronia bombardensis (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia bombardensis* Urb. et Ekm. Ark. Bot. 22 A 17:86. 1929.

Varronia bonplandii Desv. Journ. Bot. 1:275. 1808. — Venezuela

- Syn.: *Cordia bonplandii* Roem. et Schult. 1819.

Verronia braceliniae (I. M. Johnst.) Borhidi comb. nova — Brazil

- Basionym: *Cordia braceliniae* I. M. Johnston J. Arn. Arb. 16: 177. 1935.

Varronia bridgesii Friesen — Bolivia

Varronia bullata L. Syst. X. ed. II. 1759. p. 916. — Jamaica

- Syn.: *Montjolya bullata* Friesen Bull. Soc. Bot. Genève Sér. II. 24:142. 1933. — *Cordia bullata* (L.) Roem. et Schult. in Linné Syst. Veg. ed. nov. 4:462. 1819.

Varronia calcicola (Urb.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia calcicola* Urb. Symb. Ant. 3:359. 1903.

Varronia calocephala (Cham.) Friesen l. c. 149. — Brazil

- Basionym: *Cordia calocephala* Cham. Linnaea 4:488. 1829.

Varronia caput-medusae (Taub.) Friesen l. c. 149. — Brazil

- Basionym: *Cordia caput-medusae* Taub. Bot. Jahrb. 15. Beibl. n. 38:15. 1893.

Varronia clarendonensis Britton Bull. Torr. Bot. Club 41:16. 1914. — Jamaica

- Syn.: *Cordia clarendonensis* (Britt.) Stearn Journ. Arn. Arb. 52:631. 1971.

Varronia claviceps (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia claviceps* Urb. et Ekm. Ark. Bot. 20 A 5:42. 1926.

Varronia coriacea Moldenke Phytologia 2:144. 1946. — Cuba

- Syn.: *Cordia van-hermannii* (Mold.) Alain Contr. Ocas. Mus. Hist. Nat. Col. La Salle 15: 12. 1956. non *Cordia coriacea* Killip 1927. nec Sagot et Benoist 1933.

Varronia coyucana (I. M. Johnst.) Borhidi comb. nova — Mexico

- Basionym: *Cordia coyucana* I. M. Johnst. J. Arn. Arb. 29:227. 1948.

Varronia dasycephala Desv. Journ. Bot. 1:274. 1808. — Mexico, W-Indies, N. of South-America

- Syn.: *Cordia dasycephala* Kunth in H. et B.

Varronia duartei (Borhidi et Muñiz) Borhidi comb. nova — Cuba

- Basionym: *Cordia duartei* Borhidi et Muñiz Acta Bot. Acad. Sci. Hung. 17:24. 1971.

Varronia fasciata (Leonard et Alain) Borhidi comb. nova — Haiti

- Basionym: *Cordia fasciata* Leonard et Alain in Alain Brittonia 20:151. 1968.

Varronia galapagensis (Guerke) Borhidi comb. nova — Galapagos

- Basionym: *Cordia galapagensis* Guerke Nat. Pflanzenfam. IV. 3:83. 1893.

- Syn.: *Varronia scaberrima* Anderss. l. c. non Bertero

Varronia gibberosa (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia gibberosa* Urb. et Ekm. Ark. Bot. 22 A 17:84. 1929.

Varronia globosa Jacq. Enum. 14. 1760. — Trop. Amer.

— Syn.: *Cordia globosa* (Jacq.) Kunth Nov. Gen. 376. 11818.

Varronia globosa Jacq. ssp. *humilis* (Jacq.) Borhidi stat. novus

— Basionym: *Varronia humilis* Jacq. Enum. 14. 1760. Sel. Stirp. 41. 1763.

— Syn.: *Cordia humilis* (Jacq.) G. Don. Den. Syst. 5:1838. *Cordia globosa* (Jacq.) Kunth var. *humilis* (Jacq.) I. M. Johnst. J. Arn. Arb. 30:98. 1959. — *Cordia globosa* ssp. *humilis* (Jacq.) Borhidi Bot. Közlem. 58/3:176. 1971.

Varronia grandiflora Desv. — Brazil, Venezuela

— Syn.: *Cordia grandiflora* (Desv.) HBK.

Varronia grisebachii (Urb.) Moldenke Phytologia 2:144. 1946.

— Basionym: *Cordia grisebachii* Urb. Sym. Ant. 5:477. 1905.

Varronia hookeriana (Guerke) Borhidi comb. nova — Galapagos

— Basionym: *Cordia hookeriana* Guerke Engl. Nat. Pflanzenfam. IV. 3:83. 1893.

— Syn.: *Varronia linearis* Anderss. Vet. Akad. Handl. Stockholm 1853:204. 1855. non *V. linearis* Pav. ex DC. Prodr. 9:493. 1845.

— *Cordia linearis* Hook. f. non DC.

Varronia iberica (Urb.) Borhidi comb. nova — Cuba

— Basionym: *Cordia iberica* Urb. Ark. Bot. 22 A 17:80 1929.

Varronia intricata (Wr. in Sauv.) Borhidi comb. nova — Cuba

— Basionym: *Cordia intricata* Wr. in Sauv. Anal. Acad. Habana 6:1868.

Varronia jeremiensis (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia jeremiensis* Urb. et Ekm. Ark. Bot. 22 A No. 17:82. 1929.

Varronia leucocalyx (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia leucocalyx* Fres. in Mart. Fl. Bras. 8:822. 1857.

Varronia leucomalla (Taub.) Borhidi comb. nova — Brazil

— Basionym: *Cordia leucomalla* Taub. Bot. Jahrb. 15. Beibl. n. 38:14. 1893.

Varronia leucophlyctis (Hook. f.) Anderss. Vet. Akad. Handl. Stockh.

1853:203. 1855. — Galapagos

— Basionym: *Cordia leucophlyctis* Hook. f. Trans. Linn. Soc. 20:199. 1851.

Varronia limicola (Brandeg.) Friesen — Mexico

Varronia Lima Desv. Journ. I. 1808:278. — Caribbean

Varronia longipedunculata Britt. et Wils. Bull. Torr. Bot. Club 50:47.

1923. — Cuba

- Syn.: *Cordia longipedunculata* (Britt. et Wils.) Urb. Ark. Bot. 22 A 17:80. 1929.

Varronia lucayana Millsp. Field. Mus. Bot. 2:311. 1909. — Bahamas

- Syn.: *Cordia lucayana* (Millsp.) Macbr. Field. Mus. Bot. 8:129. 1930. *Montjolya lucayana* (Millsp.) Friesen Bull. Soc. Bot. Genève Ser. II. 24:182.

Varronia macrocephala Desv. — Amer. trop.

- Syn.: *Cordia macrocephala* (Desv.) HBK.

Varronia microphylla Desv. Journ. Bot. I:275. 1808.

- Syn.: *Cordia microphylla* (Desv.) Roem. et Schult. Syst. IV:463. 1819.

Varronia mollissima (Killip) Borhidi comb. nova — Peru

- Basionym: *Cordia mollissima* Killip J. Wash. Acad. Sci. 17:330. 1927.

Varronia nashii (Urb. et Britt.) Borhidi comb. nova — Hispaniola

- *Cordia Nashii* Urb. et Britt. in Urban Symb. Ant. 5:476. 1905.

Varronia neowidiana (DC.) Borhidi comb. nova — Brazil

- Basionym: *Cordia neowidiana* A. DC. in DC. Prodr. 9:498. 1845.

Varronia nipensis (Urb. et Ekm.) Borhidi comb. nova — Cuba

- Basionym: *Cordia nipensis* Urb. et Ekm. Ark. Bot. 22 A 17:83. 1929.

Varronia nivea (Fres.) Borhidi comb. nova — Brazil

- Basionym: *Cordia nivea* Fres. in Mart. Fl. Bras. 8:26. 1857.

Varronia oaxacana (DC.) Friesen l. c. — Mexico

- Basionym: *Cordia oaxacana* DC. Prodr. 9:497. 1845.

Varronia passa (I. M. Johnst.) Borhidi comb. nova — Mexico

- Basionym: *Cordia passa* I. M. Johnst. J. Arn. Arb. 29:227. 1948.

Varronia paucidentata (Fres.) Friesen — Brazil

- Basionym: *Cordia paucidentata* Fres. in Mart. Fl. Bras. 8:25. 1857.

Varronia pedunculosa (Wr. in Griseb.) Borhidi comb. nova — Cuba

- Basionym: *Cordia pedunculosa* Wr. ex Griseb. Cat. Pl. Cub. 1866:209.

Varronia perroyana (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia perroyana* Urb. et Ekm. Ark. Bot. 22 A 17:84. 1929.

Varronia picardae (Urb.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia picardae* Urb. Symb. Ant. 3:360. 1902.

Varronia podocephala (Torr.) Borhidi comb. nova — Mexico, Texas

- Basionym: *Cordia podocephala* Torr. Bot. Mex. Bound 135.

Varronia poliophylla (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia poliophylla* Fres. in Mart. Fl. Bras. 8:26. 1857.

Varronia polyantha (Benth.) Friesen — Ecuador

— Basionym: *Cordia polyantha* Benth. Pl. Hartw. 121. 1839.

Varronia polycephala Lam. — Lesser Ant., S-America, Porto Rico, Hispaniola

— Syn.: *Varronia corymbosa* Desv. non *Lantana corymbosa* L., nec
Cordia corymbosa (Desv.) G. Don, — *Cordia polycephala* (Lam.) M.
I. Johnst.

Varronia pringlei (Robins.) Friesen — Mexico

— Basionym: *Cordia pringlei* Robins. Proc. Am. Acad. 26:169. 1891.

Varronia revoluta (Hook. f.) Borhidi comb. nova — Galapagos

— Basionym: *Cordia revoluta* Hook. f. Trans. Linn. Soc. 20:199. 1851.

Varronia rupicola (Urb.) Britton — Puerto Rico, Hispaniola

— Basionym: *Cordia rupicola* Urb.

Varronia rusbyi (Britt.) Borhidi comb. nova — Bolivia

— Basionym: *Cordia rusbyi* Britt. ex Rusby Mem. Torr. Bot. Club 6:83.
1899.

Varronia sauvallei (Urb.) Borhidi comb. nova — Cuba

— Basionym: *Cordia sauvallei* Urb. Symb. Ant. 5:477. 1908.

Varronia scouleri (Hook. f.) Borhidi comb. nova — Galapagos

— Basionym: *Cordia scouleri* Hook. f. Trans. Linn. Soc. 20:200. 1851.

Varronia selleana (Urb.) Friesen — Hispaniola

— Basionym: *Cordia selleana* Urb. Symb. Ant. 7:346. 1912.

Varronia sessilifolia (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia sessilifolia* Cham. Linnaea 4:488. 1829.

Varronia setulosa (Alain) Borhidi comb. nova — Cuba

— Basionym: *Cordia setulosa* Alain Contr. Ocas. Mus. Hist. Nat. Col.
La Salle 15:11. 1956.

Varronia stellata (Greenm.) Borhidi comb. nova — Mexico

— Basionym: *Cordia stellata* Greenm. Proc. Amer. Acad. 39:86. 1903.

Varronia striata (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia striata* Fres. in Mart. Fl. Bras. 8:23. 1857.

Varronia subtruncata (Rusby) Friesen — Columbia

— Basionym: *Cordia subtruncata* Rusby Pl. S. Amer. 105. 1920.

Varronia toaensis (Borhidi et Muñiz) Borhidi comb. nova — Cuba

— Basionym: *Cordia toaensis* Borhidi et Muñiz Acta Bot. Acad. Sci.
Hung. 17:24. 1971.

Varronia truncata (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia truncata* Fres. in Mart. Fl. Bras. 8:25. 1857.

Varronia urticacea (Standl.) Friesen — Mexico

— Basionym: *Cordia urticacea* Standl. Contr. U. S. Nat. Herb. 23:222. 1924.

Varronia utemarkiana (Borhidi) Borhidi comb. nova — Cuba

— Basionym: *Cordia utemarkiana* Borhidi Acta Bot. Acad. Sci. Hung. 17:25. 1971.

Varronia villicaulis (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia villicaulis* Fres. in Mart. Fl. Bras. 8:24. 1857.

Varronia sect. Ulmarronia

(Sectio: Subcapitatae)

Varronia ambigua (Schlecht. et Cham.) Borhidi comb. nova — Mexico

— Basionym: *Cordia ambigua* Schlecht. et Cham. Linnaea 5:115. 1830.

Varronia cana (Mart. et Gal.) Borhidi comb. nova — Mexico

— Basionym: *Cordia cana* Mart. et Gal. Bull. Acad. Brux. 11/2:331. 1844.

Varronia candolleana Borhidi nom. novum — Brazil

— Basionym: *Cordia longifolia* A. DC. in DC. Prodr. 9:495. 1845.
non *Varronia longifolia* Sessé et Moc. 1893.

Varronia corchorifolia (DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia corchorifolia* A. DC. in DC. Prodr. 9:496. 1845.

Varronia corymbosa (L.) Desv. — Jamaica, C-Amer.

— Syn.: *Lantana corymbosa* L. Spec. I. ed. II. 1753. p. 628.
— *Cordia corymbosa* (L.) G. Don Gen. Syst. IV:383. 1838.
— *Varronia corymbosa* (L.) Desv., — *Cordia linnaei*
Stearn

Varronia crenata Ruiz et Pav. — Peru

Varronia dichotoma Ruiz et Pav. — Amer. trop.

Varronia discolor (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia discolor* Cham. Linnaea 4:482. 1829.

Varronia erythrococca (Wr. ex Griseb.) Moldenke — Cuba

— Basionym: *Cordia erythrococca* Wr. ex Griseb. Cat. Pl. Cub. 1866:208.

Varronia fasciculata (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia fasciculata* Urb. et Ekm. Ark. Bot. 20 A 5:43. 1926.

Varronia foliosa (Mart. et Gal.) Borhidi comb. nova — Mexico

- Basionym: *Cordia foliosa* Mart. et Gal. Bull. Acad. Brux. 11/2:330. 1844.

Varronia hermanniifolia (Cham.) Borhidi comb. nova — Mexico

- Basionym: *Cordia hermanniifolia* Cham. Linnaea 4:484. 1829.

Varronia inermis (Mill.) Borhidi comb. nova — Mexico

- Basionym: *Cordia inermis* Miller Dict. 1768.

Varronia lanceolata (HBK.) Borhidi comb. nova — Colombia

- Basionym: *Cordia lanceolata* HBK. Nov. Gen. et Sp. 3:75. 1818.

Varronia mariyuitensis (HBK.) Borhidi comb. nova — Colombia

- Basionym: *Cordia mariyuitensis* HBK. Nov. Gen. et Sp. 3:75. 1818.

Varronia microcephala (Willd. in Roem. et Schult.) Borhidi comb. nova —

C-America — Venezuela

- Basionym: *Cordia microcephala* Willd. in Roem. et Schult. Syst. Veg. 4:801. 1819.

Varronia moensis Moldenke Phytologia 2:145. — Cuba

- Syn.: *Cordia moensis* (Mold.) Alain Contr. Ocas. Mus. Hist. Nat. Col. La Salle No. 15:11. 1956.

Varronia parviflora (Ortega) Borhidi comb. nova — Mexico

- Basionym: *Cordia parviflora* Ortega Hort. Matr. 85.

Varronia patens (HBK.) Borhidi comb. nova — Brazil

- Basionym: *Cordia patens* HBK. Nov. Gen. et Sp. 3:75. 1818.

Varronia salvifolia (Juss. ex Poir.) Borhidi comb. nova — Lesser Antilles

- Basionym: *Cordia salvifolia* Juss. ex Poir. Encycl. 7:46. 1806.

Varronia sect. Montjolya

Varronia acuta (Pittier) Borhidi comb. nova — Colombia

- Basionym: *Cordia acuta* Pittier Contrib. U. S. Nat. Herb. 18:252. 1917.

Varronia angustifolia West in Willd. Spec. Pl. 1:1081. 1797.

- Syn.: *Cordia angustifolia* Roem et Schult. Syst. 4:460. 1819. non Roxb. 1814. — *Cordia stenophylla* Alain Contr. Ocas. Mus. Hist. Nat. Col. La Salle No. 15:12. 1956. — *Montjolya angustifolia* (West in Willd.) Friesen in Bull. Soc. Bot. Genève Ser. II. 24:180. 1933.

Varronia aubletii (DC.) Borhidi comb. nova — Guyana

- Basionym: *Cordia aubletii* DC. Prodr. 2:490. 1845.

Varronia bahiensis (DC.) Borhidi comb. nova — Brazil

- Basionym: *Cordia bahiensis* DC. Prodr. 9:489. 1845.

Varronia bellonis (Urb.) Borhidi comb. nova — Puerto Rico

- Basionym: *Cordia bellonis* Urb. Symb. Ant. 1:393. 1900.

Varronia bifurcata (Roem. et Schult.) Borhidi comb. nova — Colombia

- Basionym: *Cordia bifurcata* Roem. et Schult. Syst. Veg. 4:466. 1819.
- Syn.: *Cordia corymbosa* auct. non (L.) G. Don; *C. corymbosa* var. *detensa* I. M. Johnst.

Varronia boliviana (Gand.) Borhidi comb. nova — Bolivia

- Basionym: *Cordia boliviana* Gandoger Bull. Soc. Bot. France 65:62. 1918.

Varronia brevispicata (Mart. et Gal.) Borhidi comb. nova — Mexico

- Basionym: *Cordia brevispicata* Mart. et Gal. Bull. Acad. Brux. 11/2:331. 1844.

Varronia brittonii Millsp. Field Col. Mus. Bot. II.311. 1909.Varronia brownei (Friesen) Borhidi comb. nova — Jamaica

- Basionym: *Montjolya brownei* Friesen Bull. Soc. Bot. Genève 931-2. Sér. II. 24:142. 1933.
- Syn.: *Cordia brownei* (Friesen) I. M. Johnston Journ. Arn. Arb. 31:177. 1950.

Varronia campestris (Warm) Borhidi comb. nova — Brazil

- Basionym: *Cordia campestris* Warm Kjoeb. Videntk. Meddel. 12. 1867.

Varronia canescens (HBK.) Borhidi comb. nova — Colombia

- Basionym: *Cordia canescens* HBK. Nov. Gen. et Sp. 3:73. 1818.

Varronia caracasana (DC.) Borhidi comb. nova — Venezuela

- Basionym: *Cordia caracasana* DC. Prodr. 9:489. 1845.

Varronia chacoensis (Chodat) Borhidi comb. nova — Paraguay

- Basionym: *Cordia chacoensis* Chodat Bull. Soc. Bot. Genève sér. 2. 1920. 12:218. (1921)

Varronia cinerascens (A. DC.) Borhidi comb. nova — W-Indies

- Basionym: *Cordia cinerascens* A. DC. in DC. Prodr. 9:492. 1845.
- Syn.: *Cordia cylindrostachya* auct. non Ruiz et Pavón

Varronia coloradiphila (Gilli) Borhidi comb. nova — Ecuador

- Basionym: *Cordia coloradiphila* Gilli Feddes Rep. 94:304. 1983.

Varronia corallicola (Urb.) Borhidi comb. nova — Hispaniola

- Basionym: *Cordia corallicola* Urb. Ark. Bot. 22 A 17:79. 1929.

- Varronia costaricensis (I. M. Johnst.) Borhidi comb. nova — Costa Rica
— Basionym: *Cordia costaricensis* I. M. Johnst. J. Arn. Arb. 30:103. 1949.
- Varronia crenulata (DC.) Friesen — Mexico
— Basionym: *Cordia crenulata* A. DC. in DC. Prodr. 9:492. 1845.
- Varronia cuneiformis (DC.) Borhidi comb. nova — Venezuela
— Basionym: *Cordia cuneiformis* DC. Prodr. 9:492. 1845.
- Varronia curassavica Jacq.
- Varronia cylindrostachya Ruiz et Pavon Flor. Peru II.23. 1799. — Trop. Amer.
— Syn.: *Cordia cylindrostachya* (Ruiz et Pav.) Roem. et Schult. Syst. IV:459. 1819. — *Cordia angustifolia* Roem. et Schult. l. c. 460. non Roxb. — *Montjolya cylindrostachya* (R. et P.) Friesen Bull. Soc. Bot. Genève, Ser. II. 24:181. 1933.
- Varronia divaricata (HBK.) Borhidi comb. nova — Lesser Antillas, Venezuela
— Basionym: *Cordia divaricata* HBK. Nov. Gen. et Sp. 3:74. 1818.
- Varronia ewanii (Killip) Borhidi comb. nova — Colombia
— Basionym: *Cordia ewanii* Killip
- Varronia exarata (Urb.) Borhidi comb. nova — Hispaniola
— Basionym: *Cordia exarata* (Urb.) Symb. Ant. 3:358. 1903.
- Varronia ferruginea Lam.
- Varronia floribunda Desv. — Brazil
— Syn.: *Cordia floribunda* Spreng. Syst. Veg. 1:652. 1825.
- Varronia glandulosa (Fres.) Borhidi comb. nova — Brazil
— Basionym: *Cordia glandulosa* Fres. in Mart. Fl. Bras. 8:19. 1857.
- Varronia graveolens (HBK.) Borhidi comb. nova — Brazil, Colombia
— Basionym: *Cordia graveolens* HBK. Nov. Gen. et Sp. 3:374. 1818.
- Varronia guianensis Desv. — Guyana
- Varronia haitiensis (Urb.) Borhidi comb. nova — Hispaniola
— Basionym: *Cordia haitiensis* Urb. Symb. Ant. 3:357. 1903.
- Varronia hispida (Benth.) Borhidi comb. nova — C-America
— Basionym: *Cordia hispida* Benth. Bot. Voy. Sulph. 139.
- Varronia holguinensis (Borhidi et Muñiz) Borhidi comb. nova — Cuba
— Basionym: *Cordia holguinensis* Borhidi et Muñiz Acta Bot. Acad. Sci. Hung. 22:316. 1976.

Varronia integrifolia Desv. Journ. Bot. I:271. t. 10 — Caribbean

- Syn.: *Cordia integrifolia* (Desv.) Roem. et Schult. Syst. IV:461. 1819. — *Montjolya integrifolia* (Desv.) Friesen Bull. Soc. Bot. Genève Sér. II. 24:181. 1933.

Varronia interrupta (DC.) Borhidi comb. nova — Brazil, Venezuela

- Basionym: *Cordia interrupta* DC. Prodr. 9:491. 1845.

Varronia jamaicensis (I. M. Johnst.) Borhidi comb. nova — Jamaica

- Basionym: *Cordia jamaicensis* I. M. Johnst. Journ. Arn. Arb. 31:178. 1950.

Varronia lanata (HBK.) Borhidi comb. nova — Colombia

- Basionym: *Cordia lanata* HBK. Nov. Gen. et Sp. 3:72. 1818.

Varronia laxiflora (HBK.) Borhidi comb. nova — Mexico — Peru

- Basionym: *Cordia laxiflora*. HBK. Nov. Gen. et Sp. 3:72. 1818.

Varronia lenis (Alain) Borhidi comb. nova — Cuba

- Basionym: *Cordia lenis* Alain Contr. Ocas. Mus. Hist. Nat. Col. La Salle 15:10. 1956.

Varronia leptoclada (Urb. et Britt.) Millsp. Publ. Field. Columb. Must. Bot. II. 310. 1909. — Cuba — Hispaniola — Porto Rico

- Basionym: *Cordia leptoclada* Urb. et Britt. Smyb. Ant. 5:478. 1905.
- Syn.: *Cordia angustifolia* Griseb. non Roem. et Schult.

Varronia linearis Pav. ex DC. — Mexico

- Syn.: *Cordia linearis* A. DC. in DC. Prodr. 9:493. 1845.

Varronia macrostachya Jacq. — Columbia

- Syn.: *Cordia macrostachya* (Jacq.) Roem. et Schult.

Varronia martinicensis Jacq. — Lesser Antilles

Varronia mollis West ex DC.

Varronia multispicata (Chem.) Borhidi comb. nova — Brazil

- Basionym: *Cordia multispicata* Cham. Linnaea 4:499. 1829.

Varronia nesophila (I. M. Johnst.) Borhidi comb. nova — Santa Lucia

- *Cordia nesophila* I. M. Johnst. J. Arn. Arb. 37:289. 1956.

Varronia oxyphylla (DC.) Borhidi comb. nova — Guyana

- Basionym: *Cordia oxyphylla* DC. Prodr. 9:492. 1845.

Varronia paraguariensis (Chod. et Hassl.) Borhidi comb. nova — Paraguay

- Basionym: *Cordia paraguariensis* Chodat et Hassl. Bull. Herb. Boiss. sér. 2. 5:305. 1905.

Varronia pauciflora (Rusby) Borhidi comb. nova — Bolivia

— Basionym: *Cordia pauciflora* Rusby Mem. Torr. Bot. Cl. 6:83. 1896.

Varronia peruviana (Roem. et Schult.) Borhidi comb. nova — Mexico — Peru

— Basionym: *Cordia peruviana* Roem. et Schult. Syst. 4:459. 1819.

Varronia poeppigii (DC.) Borhidi comb. nova — Peru

— Basionym: *Cordia poeppigii* DC. Prodr. 9:492. 1845.

Varronia polystachya (HBK.) Borhidi comb. nova — Venezuela

— Basionym: *Cordia polystachya* HBK. Nov. Gen. et Sp. 3:73. 1818.

Varronia riparia (HBK.) Borhidi comb. nova — C-America

— Basionym: *Cordia riparia* HBK. Nov. Gen. et Sp. 3:71. 1818.

Varronia rosei (Killip) Borhidi comb. nova — Ecuador

— Basionym: *Cordia rosei* Killip J. Wash. Acad. Sci. 17:330. 1927.

Varronia salicina (DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia salicina* DC. Prodr. 9:492. 1845.

Varronia schomburgkii (DC.) Borhidi comb. nova — Guiana

— Basionym: *Cordia schomburgkii* DC. Prodr. 9:490. 1845.

Varronia shaferi Britton Mem. Torr. Club 16: 95. 1920. — Cuba

— Syn.: *Cordia shaferi* (Britt.) Alain

Varronia spinescens (L.) Borhidi comb. nova — Trop. Amer.

— Basionym: *Cordia spinescens* L. Mant. 2:206. 1771.

— Syn.: *Varronia ferruginea* Lam. 1791. — *Varronia crenulata* Sessé et Mocino Fl. Mex. 48. 1893.

Varronia suffruticosa (Borhidi) Borhidi comb. nova — Cuba

— Basionym: *Cordia suffruticosa* Borhidi Acta Bot. Acad. Sci. Hung. 22:315. 1976.

Varronia tobagensis (Urb.) Borhidi comb. nova — Tobago

— Basionym: *Cordia tobagensis* Urb. Feddes Repert. 16:39. 1919.

Varronia tomentosa Lam. — Guyana

— Syn.: *Cordia tomentosa* (Lam.) Roem. et Schult.

Varronia verbenacea (DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia verbenacea* DC. Prodr. 9:491. 1845.

Varronia wagnerorum (Howard) Borhidi comb. nova — Porto Rico

— Basionym: *Cordia wagnerorum* Howard J. Arn. Arb. 47:137. 966.

Varronia sect. Cordiopsis

Varronia anisodonta (Urb.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia anisodonta* Urb. Symb. Ant. 7:348. 1912.

Varronia chabrensis (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia chabrensis* Urb. et Ekm. Ark. Bot. "" A 17:87. 1929.

Varronia dependens (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia dependens* Urb. et Ekm. Ark. Bot. 22 A 17:87 1929.

Varronia fasciculata (Urb. et Ekm.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia fasciculata* Urb. et Ekm. Ark. Bot. 20 A 5:43. 1926.

Varronia foliosa (Mart. et Gal.) Borhidi comb. nova — Mexico, Guatemala

— Basionym: *Cordia foliosa* Mart. et Gal. Bull. Acad. Brux. 11/2:330. 1844.

Varronia lamprophylla (Urb.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia lamprophylla* Urb. Symb. Ant. 7:346. 1912.

Varronia oligodonta (Urb.) Borhidi comb. nova — Hispaniola

— Basionym: *Cordia oligodonta* Urb. Symb. Ant. 7:347. 1912.

Varronia serrata (L.) Borhidi comb. nova — Greater Antilles

— Basionym: *Tournefortia serrata* L. Spec. Plant. I. ed. I. 1753.p.140.

— Syn.: *Varronia bullata* L. Spec. II. ed. I. 1762. p. 276.

Varronia mirabilioides Jacq., *Cordia mirabilioides* (Jacq.) Roem. et Schult.

Gerascanthus P. Browne

Civ. Nat. Hist. Jamaica 170. 10. Mart. 1756; sectio *Gerascanthus* Cham. in *Linnaea* 1829: 171; *Cerdana Ruiz et Pav. Fl. Peru. Prodr.* p. 37. t. 6. 1794; section *Rhabdocalyx* A. DC. in DC. Prodr. 9:474. 1845; section *Pilicordia* A. DC. in DC. Prodr. 9:474. 1845; section *Physoclada* DC. Prodr. 9:475. 1845; section *Myxa* Endl. Gen. Plant. p. 644. 1840; *Varronia* DC. Prodr. 9:468. 1845, non P. Browne; *Myxa* Friesen Bull. Soc. Bot. Genève 24:136. 1933; *Collococcus* P. Browne l. c. 167. 1756; *Calyptrocordia* Britt. in *Britt et Millsp. Sci. Surv. Porto Rico* 6:122. 1925.

The rest of the species belonging to the widely considered *Cordia* is a rather varied group. Several attempts have been made to divide it into several genera, as it was suggested by DE CANDOLLE (1845), BRITTON (1925) and FRIESEN (1933). Features for differentiating them, the form and opening

of flower buds, ribbed or unribbed calyx, size and texture of the corolla have been considered. When analyzing the occurrence of these features represented in a larger number of the species, we experience them occurring in several different combinations overlapping over the different taxonomic groups. So these morphological evidences seem to be insufficient for dividing this group into several genera. The great majority of the species show an irregular opening of the calyx, producing a continuous intermediate range between regular opening of Cordia gerascanthus to the calyptriform disruption of the buds in the Cordia alba. Consequently I support a decision not to split further the remained group of Cordia, and unit them under well marked and described early generic name, which is Gerascanthus P. Browne.

The most important common characteristic features of this re-vali-dated genus are the following:

Tropical trees and shrubs with alternate leaves, the flowers are grouped into mostly large loose cymose-corymbose terminal, sometimes axillary inflorescences. Calyx oblong-elliptic, oblanceolate or obovate, sometimes ribbed with strong nerves, mostly smooth. Flower buds mostly rounded, sometimes apiculate, calyx lobes without thickened margin, opening mostly irregularly or with short lobes, they are mostly membraneous or filmy. Flowers medium sized or small, often dichogamous or functionally monosexual, 5-merous, with fertile ovary and sterile stamens and vice versa. Cleistogamy is also a common feature. Stamens with ovate or quadrate anthers. Pistil bifurcate or twice bifurcate. Pollen grains tricolpate, 3-colporate or 3-colporoidate, with short colpi. Sexine tectate provided by mostly acute, spiny, sometimes rounded or rarely mixed processes or protuberances. (Sterile pollen may be microverrucated.) Pollen kit abundant often hiding the outer structure of the pollen, sticky, maintaining the pollen grains in a pollinium-like sticky conglomeration.

Typus generis: Cordia gerascanthus L. Syst. Nat. ed. 10. 2: 936. 1759.

The genus includes about 160-180 species from tropical America, Asia, Africa and Oceania.

According to the view of Taroda and Gibbs (1986a) we share their consideration about the subgeneric rank of Gerascanthus and Myxa with the slight difference, namely under the genus Gerascanthus separated of Cordia.

1. Subgenus: Gerascanthus

Syn.: Cerdana Ruiz et Pav. Prodr. 37. 1794.; Cordiada Vellozo, Fl. Flum. 98. 1829; Icones 2: 156. 1831.; Cordia subgen. Gerascanthus Cham., Linnaea 5: 115. 1831.; Cordia sect. Cerdanae

(Ruiz et Pav.) Roem. et Schult., Syst. 4:499. 1818.

2. Subgenus: Myxa (Taroda) Borhidi comb. nova

Basionym.: Myxa Taroda pro gubgen. Cordia in Taroda et Gibbs
Rev. Bras. Bot. 9: 38. 1986.

Typus subgeneris: Cordia myxa L. Sp. Pl. 1: 190. 1753.

Syn.: Collococcus P. Browne l.c. 167. 1756.; Calyptrocordia
Britton in Britt. et Wils., Sci. Surv. Porto Rico and Virgin
Islands, New York. Acad. Sci. 6: 122. 1925.

It is to be admitted, that the traditional sections do not reflect completely the real variability of this genus. First of all, the relations between the sections Pilicordia and Myxa are not clear. About this point further studies are needed.

As for the nomenclatural consequences of the above treatment the following new combinations are suggested:

Gerascanthus africanus (Lam.) Borhidi comb. nova - Afr. Trop.

- Basionym: Cordia africana Lam., Encycl. Méth. Bot. 1792: 420.

Gerascanthus alliodorus (Ruiz et Pav.) Borhidi comb. nova - Trop. Amer.

- Basionym: Cerdana alliodora Ruiz et Pav. Flor. Peruv. II.47. t.
184. 1799.

- Syn.: Cordia alliodora (Ruiz et Pav.) Cham. in Linnaea VIII. 121.
1833. - Cordia gerascanthus Jacq. Sel. Stirp. Amer. 43. 1763.

Gerascanthus aristeguietae (Agostini) Borhidi comb. nova - Venezuela

- Basionym: Cordia aristeguietae Agostini Phytologia 39(6):433.
1978.

Gerascanthus asterophorus (Mart.) Borhidi comb. nova - Brazil

- Basionym: Cordia asterophora Mart. ex Fresen in Mart. Fl. Bras.
8:5. 1857.

Gerascanthus atro-fuscus (Taub.) Borhidi comb. nova - Brazil

- Basionym: Cordia atro-fusca Taub. Bot. Jahrb. 15. Beibl. no. 38:12.
1893.

Gerascanthus chamissonianus (Steud.) Borhidi comb. nova - Brazil

- Basionym: Cordia chamissoniana Steud. Nom. ed. II. 1:417.

Gerascanthus colimensis (I. M. Johnst.) Borhidi comb. nova - Mexico

- Basionym: Cordia colimensis I. M. Johnst. J. Arn. Arb. 31:186. 1950.

Gerascanthus cujabensis (Manso et Lhotzky) Borhidi comb. nova - Brazil

- Basionym: Cordia cujabensis Manso et Lhotzky ex Cham. Linnaea
8:12. 1833.

Gerascanthus elaeagnoides (A. DC.) Borhidi comb. nova — Mexico

— Basionym: *Cordia elaeagnoides* A. DC. in DC. Prodr. 9:474. 1845.

Gerascanthus excelsus (A. DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia excelsa* A. DC. in DC. Prodr. 9:473. 1845.

Gerascanthus fawcettii (Kr. et Urb.) Borhidi comb. nova — Jamaica

— Basionym: *Cordia fawcettii* Kr. et Urb. Symb. Ant. 1:391. 1900.

Gerascanthus gerascanthoides (HBK.) Borhidi comb. nova — Trop. Amer.

— Basionym: *Cordia gerascanthoides* HBK. Kunth. in H. et B. Nov. Gen. III: 83. 1818.

— Syn: *Cordia gerascanthus* L. Syst. Nat. ed. 10. 2:936. 1759.

Gerascanthus glabratus (A. DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia glabrata* A. DC. in DC. Prodr. 9:473. 1845.

Gerascanthus globuliferus (I. M. Johnst.) Borhidi comb. nova — Mexico

— Basionym: *Cordia globulifera* I. M. Johnst. J. Arn. Arb. 31:184. 1950.

Gerascanthus goeldianus (Huber) Borhidi comb. nova — Brazil

— Basionym: *Cordia goeldiana* Huber Mus. Bot. Para. 6:89. 1910.

Gerascanthus gracilipes (I. M. Johnst.) Borhidi comb. nova — Mexico

— Basionym: *Cordia gracilipes* I. M. Johnst. J. Arn. Arb. 31:186. 1950.

Gerascanthus guerkeanus (Loes.) Borhidi comb. nova — Mexico

— Basionym: *Cordia guerkeana* Loes. Verh. Bot. Ver. Brandenbg. 55:186. 1913.

Gerascanthus haenkeanus (Mez) Borhidi comb. nova — Peru

— Basionym: *Cordia haenkeana* Mez Bot. Jahrb. 12:560. 1890.

Gerascanthus harrisii (Urb.) Borhidi comb. nova — Jamaica

— Basionym: *Cordia harrisii* Urb. Symb. Ant. 5:474. 1904.

Gerascanthus hypoleucus (A. DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia hypoleuca* A. DC. in DC. Prodr. 9:472. 1845.

Gerascanthus iguaguanus (I. M. Johnst.) Borhidi comb. nova — Peru

— Basionym: *Cordia iguaguana* I. M. Johnst. J. Arn. Arb. 33:63. 1952.

Gerascanthus igualensis (Bartlett) Borhidi comb. nova — Mexico

— Basionym: *Cordia igualensis* Bartlett Contr. Gray Herb. 36:632. 1909.

Gerascanthus insignis (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia insignis* Cham. Linnaea 8:122. 1833.

Gerascanthus longipedus (Mez) Borhidi comb. nova — Brazil

— Basionym: *Cordia longipeda* Mez Bot. Jahrb. 12:550. 1890.

Gerascanthus luteus (Lam.) Borhidi comb. nova — Galapagos

— Basionym: *Cordia lutea* Lam. Tabl. Encycl. 1:421. 1791.

Gerascanthus megalanthus (Blake) Borhidi comb. nova — Guatemala

— Basionym: *Cordia megalantha* Blake Proc. Biol. Soc. Wash. 36:200. 1923. — *Cordia macrantha* Blake not Chodat

Gerascanthus morelosanus (Standl.) Borhidi comb. nova — Mexico

— Basionym: *Cordia morelosana* Standl. Contr. US. Nat. Herb. 23:1220. 1927.

Gerascanthus nelsonii (I. M. Johnst.) Borhidi comb. nova — Mexico

— Basionym: *Cordia nelsonii* I. M. Johnst. J. Arn. Arb. 31:183. 1950.

Gerascanthus nettoanus (Taub.) Borhidi comb. nova — Brazil

— Basionym: *Cordia nettoana* Taub. Bot. Jahrb. 15. Beibl. no. 38:11. 1893.

Gerascanthus petenensis (Lundell) Borhidi comb. nova — Guatemala

— Basionym: *Cordia petenensis* Lundell Wrightia 4:49. 1968.

Gerascanthus rufescens (A. DC.) Borhidi comb. nova — S. America

— Basionym: *Cordia rufescens* A. DC. in DC. Prodr. 9:476. 1845.

Gerascanthus sonorae (Rose) Borhidi comb. nova — Mexico

— Basionym: *Cordia sonorae* Rose Contr. US. Nat. Herb. 1:106. t. 9. 1891.

Gerascanthus tinifolius (Willd. ex Roem. et Schult.) Borhidi comb. nova — Mexico

— Basionym: *Cordia tinifolia* Willd. ex Roem. et Schult. Syst. 4:801. 1819.

Gerascanthus trichotomus (Vell.) Borhidi comb. nova — Brazil

— Basionym: *Cordia trichotoma* Vell. ex Steud. Nom. ed. 2. 1:419.

Gerascanthus troyanus (Urb.) Borhidi comb. nova — Jamaica

— Basionym: *Cordia troyana* Urb. Symb. Ant. 5:475. 1904.

Gerascanthus varroniifolius (I. M. Johnst.) Borhidi comb. nova — Peru

— Basionym: *Cordia varroniifolia* M. I. Johnst. J. Arn. Arb. 33:62. 1952.

Subgenus: Myxa (Taroda) Borhidi

Neotropical species:

Gerascanthus acutifolius (Fres.) Borhidi comb. nova — Brazil

— Basionym: *Cordia acutifolia* Fres. in Mart. Fl. Bras. 8:11. 1857.

Gerascanthus anabaptista (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia anabaptista* Cham. *Linnaea* 8:512. 1833.

Gerascanthus bicolor (A. DC.) Borhidi comb. nova — Centr. Amer.

— Basionym: *Cordia bicolor* A. DC. *Prodr.* 2:485. 1845.

Gerascanthus bifurcatus (Roem. et Schult.) Borhidi comb. nova — W-Indies

— Basionym: *Cordia bifurcata* Roem. et Schult. in I. *Syst. Veg.* ed. nov. 4:466. 1819.

Gerascanthus bogotensis (Benth.) Borhidi comb. nova — Colombia

— Basionym: *Cordia bogotensis* Benth. *Pl. Hartw.* 240. 1845.

Gerascanthus borinquensis (Urb.) Borhidi comb. nova — Porto Rico

— Basionym: *Cordia borinquensis* Urb. *Symb. Ant.* 1:390. 1900.

Gerascanthus brachypodus (DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia brachypoda* DC. *Prodr.* 2:487. 1845.

Gerascanthus calophyllus (Vahl) Borhidi comb. nova — Guyana

— Basionym: *Cordia calophylla* Vahl *Eclog. Amer.* 315. 1807.

Gerascanthus collococcus (L.) Borhidi comb. nova — Caribbean

— Basionym: *Cordia collococca* L. *Fl. Jam.* 14. 1759.

Gerascanthus colombianus (Killip) Borhidi comb. nova — Colombia

— Basionym: *Cordia colombiana* Killip *J. Wash. Acad. Sci.* 17:327. 1927.

Gerascanthus cordifolius (HBK.) Borhidi comb. nova — Colombia

— Basionym: *Cordia cordifolia* HBK. *Nov. Gen. et Spec.* 3:70. 1818.

Gerascanthus cordiformis (Johnst.) Borhidi comb. nova — Guatemala

— Basionym: *Cordia cordiformis* Johnst. *J. Arn. Arb.* 18:10. 1937.

Gerascanthus cymosus (Donn.-Sm.) Borhidi comb. nova — Costa Rica — Panama

— Basionym: *Cornutia cymosa* Donn.-Sm. *Bot. Gaz.* 40:10. 1905.

Gerascanthus decipiens (I. M. Johnst.) Borhidi comb. nova — Brazil

— Basionym: *Cordia decipiens* I. M. Johnston *J. Arn. Arb.* 18:11. 1937.

Gerascanthus diversifolius (Pav. ex DC.) Borhidi comb. nova — C-America

— Basionym: *Cordia diversifolia* Pav. ex DC. *Prodr.* 2:474. 1845.

Gerascanthus dwyeri (Nowicke) Borhidi comb. nova — C-America

— Basionym: *Cordia dwyeri* Nowicke *Phytologia* 18:419. 1969.

Gerascanthus ecalyculatus (Vell.) Borhidi comb. nova — Brazil

— Basionym: *Cordia ecalyculata* Vell. *Fl. Flum.* 96. 2. t. 140.

Gerascanthus ellipticus (Sw.) Borhidi comb. nova — W-Indies

— Basionym: *Cordia elliptica* Sw. *Nov. Gen. et Spec. Pl.* 47. 1788.

Gerascanthus exaltatus (Lam.) Borhidi comb. nova — Guyana

— Basionym: *Cordia exaltata* Lam. *Illustr. l. n.* 1919. 1791.

Gerascanthus eriostigma (Pittier) Borhidi comb. nova — Costa Rica

- Basionym: *Cordia eriostigma* Pittier Contr. US. Nat. Herb. 18:251. fig. 101. 1917.

Gerascanthus flavescens (Aubl.) Borhidi comb. nova — Guyana

- Basionym: *Cordia flavescens* Aubl. Pl. Guian. 1:226. t. 89. 1775.

Gerascanthus grandifolius (A. DC.) Borhidi comb. nova — Brazil

- Basionym: *Cordia grandifolia* A. DC. in -DC. Prodr. 9:475. 1845.

Gerascanthus hebecladus (I. M. Johnst.) Borhidi comb. nova — S-America

- Basionym: *Cordia hebeclada* I. M. Johnst. J. Arn. Arb. 31:176. 1950.

Gerascanthus heterophyllus (Roem et Schult.) Borhidi comb. nova — Guyana

- Basionym: *Cordia heterophylla* Roem et Schult. Syst. 4:800. 1819.

Gerascanthus hintoni (I. M. Johnst.) Borhidi comb. nova — Mexico

- Basionym: *Cordia hintoni* I. M. Johnst. J. Arn. Arb. 21:343. 1940.

Gerascanthus hirtus (I. M. Johnst.) Borhidi comb. nova — Venezuela

- Basionym: *Cordia hirta* I. M. Johnst. J. Arn. Arb. 16:29. 1935.

Gerascanthus inornatus (I. M. Johnst.) Borhidi comb. nova — Mexico

- Basionym: *Cordia inornata* I. M. Johnst. J. Arn. Arb. 21:341. 1940.

Gerascanthus laevigatus (Lam.) Borhidi comb. nova — W-Indies

- Basionym: *Cordia laevigata* Lam. Tabl. Encycl. et Méth. Bot. 1:422. 1792.

Gerascanthus lasiocalyx (Pittier) Borhidi comb. nova — Panama

- Basionym: *Cordia lasiocalyx* Pittier Contr. US. Nat. Herb. 18:251. 1917.

Gerascanthus latifolius (Cham.) Borhidi comb. nova — Brazil

- Basionym: *Cordia latifolia* Cham. Linnaea 8:126. 1833.

Gerascanthus lomatolobus (I. M. Johnst.) Borhidi comb. nova — Brazil

- *Cordia lomatoloba* I. M. Johnston J. Arn. Arb. 18:12. 1937.

Gerascanthus lucidulus (I. M. Johnst.) Borhidi comb. nova — C-America

- Basionym: *Cordia lucidula* I. M. Johnst. J. Arn. Arb. 21:352.

Gerascanthus macrophyllus (L.) Borhidi comb. nova — W-Indies

- Basionym: *Cordia macrophylla* L. Spec. Pl. ed. 2. I:274. 1762.

Gerascanthus magnoliifolius (Cham.) Borhidi comb. nova — Brazil

- Basionym: *Cordia magnoliifolia* Cham. Linnaea 4:476. 1829.

Gerascanthus membranaceus (A. DC.) Borhidi comb. nova — Ecuador

- Basionym: *Cordia membranacea* A. DC. in DC. Prodr. 9:484. 1845.

Gerascanthus mexianus (I. M. Johnst.) Borhidi comb. nova — Brazil

- Basionym: *Cordia mexiana* I. M. Johnston J. Arn. Arb. 18:12-13. 1937.

Gerascanthus muneco (HBK.) Borhidi comb. nova — Colombia

— Basionym: *Cordia muneco* HBK. Nov. Gen. et Sp. 7:207. 1823.

Gerascanthus naidophilus (I. M. Johnst.) Borhidi comb. nova — S-America

— Basionym: *Cordia naidophila* I. M. Johnst. J. Arn. Arb. 16:32. 1935.

Gerascanthus obscurus (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia obscura* Cham. Linnaea 13:480. 1839.

Gerascanthus ochraceus (DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia ochracea* DC. Prodr. 9:477. 1845.

Gerascanthus opacus (Rusby) Borhidi comb. nova — S. America

— Basionym: *Cordia opaca* Rusby Descr. New. Sp. S. Amer. Pl. 104.
1920.

Gerascanthus panamensis (Riley) Borhidi comb. nova — Panama

— Basionym: *Cordia panamensis* Riley Kew Bull. 1927:125. 1927.

Gerascanthus panicularis (Rudge) Borhidi comb. nova — S. America

— Basionym: *Cordia panicularis* Rudge Pl. Guian. 30. t. 46.

Gerascanthus parvifolius (A. DC.) Borhidi comb. nova — Mexico

— Basionym: *Cordia parvifolia* A. DC. Prodr. 9:498. 1845.

Gerascanthus protractus (I. M. Johnst.) Borhidi comb. nova — Panama

— Basionym: *Cordia protracta* I. M. Johnst. J. Arn. Arb. 21:349. 1940.

Gerascanthus prunifolius (I. M. Johnst.) Borhidi comb. nova — Guatemala

— Basionym: *Cordia prunifolia* I. M. Johnst. J. Arn. Arb. 21:353.
1940.

Gerascanthus pubescens (Willd.) Borhidi comb. nova — Brazil

— Basionym: *Cordia pubescens* Willd. ex Roem. et Schult. Syst. 4:800.
1819.

Gerascanthus reticulatus (Vahl) Borhidi comb. nova — Caribbean

— Basionym: *Cordia reticulata* Vahl Eclog. 3:5 1807.

Gerascanthus ripicola (I. M. Johnst.) Borhidi comb. nova — Peru

— Basionym: *Cordia ripicola* I. M. Johnston J. Arn. Arb. 16:180. 1935.

Gerascanthus rotatus (Moc.) Borhidi comb. nova — Mexico

— Basionym: *Cordia rotata* Moc. ex DC. Prodr. 9:483. 1845.

Gerascanthus salicifolius (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia salicifolia* Cham. Linnaea 4:481. 1829.

Gerascanthus sagotii (I. M. Johnst.) Borhidi comb. nova — Surinam

— Basionym: *Cordia sagotii* I. M. Johnst. J. Arn. Arb. 16:27. 1935.

Gerascanthus salvadorensis (Standl.) Borhidi comb. nova — Honduras

— Basionym: *Cordia salvadorensis* Standl. J. Wash. Acad. Sci. 14:242.
1924.

Gerascanthus scaberrimus (HBK.) Borhidi comb. nova — Peru

— Basionym: *Cordia scaberrima* HBK. Nov. Gen. et Sp. 3:71. 1818.

Gerascanthus scabridus (Mart.) Borhidi comb. nova — Brazil

— Basionym: *Cordia scabrida* Mart. ex Fres. in Mart. Fl. Bras. 8:11. 1857.

Gerascanthus scabrifolius (A. DC.) Borhidi comb. nova — Guyana

— Basionym: *Cordia scabrifolia* A. DC. in DC. Prodr. 9:485. 1845.

Gerascanthus sellowianus (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia sellowiana* Cham. Linnaea 4:479. 1829.

Gerascanthus sericalyx (A. DC.) Borhidi comb. nova — Guyana

— Basionym: *Cordia sericalyx* A. DC. in DC. Prodr. 9:485. 1845.

Gerascanthus skutchii (I. M. Johnst.) Borhidi comb. nova — Guatemala

— Basionym: *Cordia skutchii* I. M. Johnst. J. Arn. Arb. 21:339. 1940.

Gerascanthus sprucei (Mez) Borhidi comb. nova — Brazil

— Basionym: *Cordia sprucei* Mez Bot. Jahrb. 12:549. 1890.

Gerascanthus stelliferus (I. M. Johnst.) Borhidi comb. nova — C-America

— Basionym: *Cordia stellifera* I. M. Johnst. J. Arn. Arb. 21:350. 1940.

Gerascanthus stenocladus (I. M. Johnst.) Borhidi comb. nova — Mexico

— Basionym: *Cordia stenoclada* I. M. Johnst. J. Arn. Arb. 21:353. 1940.

Gerascanthus subvelutinus (I. M. Johnst.) Borhidi comb. nova — Mexico

— Basionym: *Cordia subvelutina* I. M. Johnst. J. Arn. Arb. 21:344. 1940.

Gerascanthus sulcatus (DC.) Borhidi comb. nova — W-Indies

— Basionym: *Cordia sulcata* DC. Prodr. 9:488. 1845.

Gerascanthus superbus (Cham.) Borhidi comb. nova — Brazil

— Basionym: *Cordia superba* Cham. in Linnaea 4:474. 1829.

Gerascanthus taguahuyensis (Vell.) Borhidi comb. nova — Brazil

— Basionym: *Cordia taguahuyensis* Vell. Fl. Flum. 98. 2. t. 154.

Gerascanthus tetrandrus (Aubl.) Borhidi comb. nova — Guyana, Brazil

— Basionym: *Cordia tetrandra* Aubl. Pl. Guian. 1:222. t. 87. 1775.

Gerascanthus tetraphyllus (Aubl.) Borhidi comb. nova — Guyana

— Basionym: *Cordia tetraphylla* Aubl. Pl. Guian. 1:224. t. 88. 1775.

Gerascanthus toqueve (Aubl.) Borhidi comb. nova — Guyana

— Basionym: *Cordia toqueve* Aubl. Pl. Guian. 1:228. t. 90. 1775.

Gerascanthus trachyphyllus (Mart.) Borhidi comb. nova — Brazil

— Basionym: *Cordia trachyphylla* Mart. Herb. Fl. Bras. n. 412. 1841.

Gerascanthus trichocladus (A. DC.) Borhidi comb. nova — Brazil

— Basionym: *Cordia trichoclada* A. DC. in DC. Prodr. 9:475. 1845.

Gerascanthus ucayaliensis (I. M. Johnst.) Borhidi comb. nova — Brazil

— Basionym: *Cordia ucayaliensis* I. M. Johnst. J. Arn. Arb. 16:181. 1935.

Gerascanthus ulei (I. M. Johnst.) Borhidi comb. nova — Brazil

— Basionym: *Cordia ulei* I. M. Johnston Contr. Gray Herb. n. s. 92:56. 1930.

Gerascanthus valenzuelanus (A. Rich.) Borhidi comb. nova — Cuba

— Basionym: *Cordia valenzuelana* A. Rich. in Sagra Hist. Nat. Cuba XI. 15. 1850.

Gerascanthus viridis (Rusby) Borhidi comb. nova — Venezuela

— Basionym: *Bourreria viridis* Rusby Descr. 300 So. Amer. Pl. 100. 1920.

Palaeotropical and Pantropical species:

Gerascanthus albus (Jacq.) Borhidi comb. nova

— Basionym: *Varronia alba* Jacq. Enum. Plant. Carib. 14. 1760; Select. Stirp. Amer. 41. 1763.

— Syn.: *Cordia alba* (Jacq.) Roem. et Schult. Syst. 4:466. 1819. —

Gerascanthus aurantiacus (Baker) Borhidi comb. nova — Afr. trop.

— Basionym: *Cordia aurantiaca* Baker Kew Bull. 1894:26.

Gerascanthus bakeri (Britten) Borhidi comb. nova — Afr. trop.

— Basionym: *Cordia bakeri* Britten Journ. Bot. 1895:88.

Gerascanthus balanocarpus (Brenan) Borhidi comb. nova — Tanzania

— Basionym: *Cordia balanocarpa* Brenan Kew Bull. 1949:91.

Gerascanthus batesii (Wernh.) Borhidi comb. nova — Cameroon

— Basionym: *Cordia batesii* Wernh. Journ. Bot. 54:229. 1916.

Gerascanthus bequaertii (DeWild) Borhidi comb. nova — Congo Belg.

— Basionym: *Cordia bequaertii* DeWild Rev. Zool. Afr. 9. Suppl. Bot. 88. 1921.

Gerascanthus caffra (Sond.) Borhidi comb. nova — S. Africa

— Basionym: *Cordia caffra* Sond. in Linnaea 23:81. 1850.

Gerascanthus chaetodonta (Melchior) Borhidi comb. nova — Tanzania

— Basionym: *Cordia chaetodonta* Melchior Notizbl. Bot. Gart. Berlin 11:676. 1932.

Gerascanthus cochinchinensis (Gagnep.) Borhidi comb. nova — SE-Asia

— Basionym: *Cordia cochinchinensis* Gagnep. Not. Syst. 3:35. 1914.

Gerascanthus crenatus (Del.) Borhidi comb. nova — Egypt.

— Basionym: *Cordia crenata* Delile Fl. Egypt. 195. t. 20. 1813.

Gerascanthus cumingianus (Vid.) Borhidi comb. nova — Philippines

— Basionym: *Cordia cumingiana* Vidal Phan. Cuming. Phillipp. 187.

Gerascanthus dichotomus (Forster f.) Borhidi comb. nova — SE-Asia, New

Caledonia NE-Australia

— Basionym: *Cordia dichotoma* Forster f. Prodr. 18. 1786.

Gerascanthus diffusus (Jacob) Borhidi comb. nova — India

— Basionym: *Cordia diffusa* Jacob Journ. Bombay Nat. Hist. Soc. 45:78. 1944.

Gerascanthus dioicus (Boj. ex DC.) Borhidi comb. nova — E-Africa, Malaga

— Basionym: *Cordia dioica* Boj. ex DC. Prodr. 9:481. 1845.

Gerascanthus ehretioides (Good.) Borhidi comb. nova — Afr. trop.

— Basionym: *Cordia ehretioides* Good. Journ. Bot. 47. Suppl. 2:107. 1929.

Gerascanthus faulknerae (B. Verdc.) Borhidi comb. nova — Tanzania

— Basionym: *Cordia faulknerae* B. Verdc. Bol. Soc. Brot. 53:104. 1980.

Gerascanthus fissistylus (K. Volles.) Borhidi comb. nova — Tanzania

— Basionym: *Cordia fissistyla* K. Vollesen Nord. J. Bot. 1(3):325. 1981.

Gerascanthus fragrantissimus (Kurz) Borhidi comb. nova — India

— Basionym: *Cordia fragrantissima* Kurz Prel. Rep. For. Veg. Peg. App. A. 92. 1875.

Gerascanthus fulvosus (Wight) Borhidi comb. nova — India

— Basionym: *Cordia fulvosa* Wight Icon. 4. t. 1380.

Gerascanthus furcans (I. M. Johnst.) Borhidi comb. nova — SE-Asia

— Basionym: *Cordia furcans* I. M. Johnst. J. Arn. Arb. 32:5. 1951.

Gerascanthus gharaf (Ehrenb. ex Aschers.) Borhidi comb. nova — E-Africa,

S-Asia

— Basionym: *Cordia gharaf* Ehrenb. ex Aschers. Sitzb. Naturf. Fr. Beil. 46. 1879.

Gerascanthus gillettii (Wildem) Borhidi comb. nova — Congo

— Basionym: *Cordia gillettii* Wildem Ann. Mus. Congo sér. 5. 1:71.

Gerascanthus glaziovii (Mez) Borhidi comb. nova — Brazil

- Basionym: *Patagonula glaziovii* Mez Bot. Jahrb. 12. Beibl. no. 27:17. 1890.

- Syn.: *Cordia glaziovii* (Mez) Taub.

Gerascanthus goetzei (Guerke) Borhidi comb. nova - Afr. trop.

- Basionym: *Cordia goetzei* Guerke Engl. Bot. Jahrb. 28:307.

Gerascanthus goossensii (DeWild) Borhidi comb. nova - Congo Belg.

- Basionym: *Cordia goossensii* DeWild Miss. de Briey Mayumbe 214. 1920.

Gerascanthus grandis (Roxb.) Borhidi comb. nova - India

- Basionym: *Cordia grandis* Roxb. Hort. Beng. 17. Fl. Ind. 1:593.

Gerascanthus griffithii (C. B. Clarke) Borhidi comb. nova - Malacca Pen. Thailand

- Basionym: *Cordia griffithii* C. B. Clarke In Hook. f. Fl. Brit. Ind. 4:139.

Gerascanthus guineensis (Thonn.) Borhidi comb. nova - Guinea

- Basionym: *Cordia guineensis* Thonn. in Schum. Beskr. Guin. Pl. 128.

Gerascanthus heudelotii (Baker) Borhidi comb. nova - Afr. occ.

- Basionym: *Cordia heudelotii* Baker Kew Bull. 1894:27.

Gerascanthus johnsonii (Baker) Borhidi comb. nova - Afr. trop.

- Basionym: *Cordia johnsonii* Baker in Dyer Fl. Trop. Afr. 4:11. 1913.

Gerascanthus kanehirai (Hayata) Borhidi comb. nova - Taiwan

- Basionym: *Cordia kanehirai* Hayata Icon. Pl. Formosa 6:31. 1916.

Gerascanthus kirkii (Baker) Borhidi comb. nova - Zambesia

- Basionym: *Cordia kirkii* Baker Kew Bull. 1894:28.

Gerascanthus macleodii (Hook. f. ex Thonn.) Borhidi comb. nova - India

- Basionym: *Cordia macleodii* Hook. f. et Thoms. J. Linn. Soc. 2:128 1858.

Gerascanthus mairei (Humbert) Borhidi comb. nova - Afr. trop.

- Basionym: *Cordia mairei* Humbert Mem. Soc. Hist. Nat. Afr. Nordhous-sér. 2:173. 1949.

Gerascanthus mhaya (Kerr) Borhidi comb. nova - Burma, Siam

- Basionym: *Cordia mhaya* Kerr Kew Bull. 1940:184.

Gerascanthus micronesicus (Kanehira et Hatusima) Borhidi comb. nova - Ins. Pulau

- Basionym: *Cordia micronesica* Kanehira et Hatusima Bot. Mag. Tokyo 53:157. 1940.

Gerascanthus millenii (Baker) Borhidi comb. nova - E. Afr. - S. Asia

- Basionym: *Cordia millenii* Baker Kew Bull. 1894:27.

Gerascanthus moluccanus (Roxb.) Borhidi comb. nova — SE-Asia

— Basionym: *Cordia moluccana* Roxb. Hort. Beng. 84., Fl. Ind. 2:594.

Gerascanthus molundensis (Mildbr.) Borhidi comb. nova — Cameroon

— Basionym: *Cordia molundensis* Mildbr. in Wiss. Ergebn. Deutsch. Zentr. Afr. Exped. 1910-11. 2:34. 1922.

Gerascanthus monoicus (Roxb.) Borhidi comb. nova — India

— Basionym: *Cordia monoica* Roxb. Pl. Corom. 1:43, t. 58.

Gerascanthus mukuensis (Taton) Borhidi comb. nova — Zaire

— Basionym: *Cordia mukuensis* Taton Bull. Jard. Bot. Nat. Belg. 41(2):258. 1971.

Gerascanthus myxus (L.) Borhidi comb. nova — Paleotropics, Africa, Asia, Australia

— Basionym: *Cordia myxa* L. Sp. Pl. 190. 1753.

— Syn.: *Cordia obliqua* Willd.; *C. domestica* Roth ex Roem. et Schult.

Gerascanthus nevillei (Alston) Borhidi comb. nova — Trop. Afr.-Asia

— Basionym: *Cordia nevillei* Alston in Trimen Handb. Fl. Ceyl. Suppl. 1931: 199.

Gerascanthus oblongifolius (Thwait.) Borhidi comb. nova — Ceylon

— Basionym: *Cordia oblongifolia* Thwait. Enum. Pl. Zeyl. 214.

Gerascanthus obovatus (Balf. f.) Borhidi comb. nova — Socotra

— Basionym: *Cordia obovata* Balf. f. Proc. Roy. Soc. Edinb. 12:80. 1884.

Gerascanthus obtusus (Balf. f.) Borhidi comb. nova — Socotra

— Basionym: *Cordia obtusa* Balf. f., Diagn. Pl. Nov. Phan. Socot. 1883: 80.

Gerascanthus perbellus (Mildbr.) Borhidi comb. nova — Cameroon

— Basionym: *Cordia perbella* Mildbr. Feddes Rep. 18:98. 1922.

Gerascanthus pilosissimus (Baker) Borhidi comb. nova — Angola

— Basionym: *Cordia pilosissima* Baker Kew Bull. 1894:28.

Gerascanthus populifolius (Baker) Borhidi comb. nova — Afr. occ.

— Basionym: *Cordia populifolia* Baker Kew Bull. 1894:27.

Gerascanthus roxburghii (C. B. Clarke) Borhidi comb. nova — Ceylon

— Basionym: *Cordia roxburghii* C. B. Clarke in Hook. f. Fl. Brit. Ind. 4:139.

Gerascanthus sinensis (Lam.) Borhidi comb. nova — Trop. Afr. — Asia

— Basionym: *Cordia sinensis* Lam. Encycl. Méth. Bot. 1792: 423.

Syn.: *Cordia gharaf* Ehrenb. ex Aschers.; *C. subopposita* DC.;

C. reticulata Roth ex Roem. et Schult.; *C. angustifolia* Roxb.;

C. senegalensis Juss.; *C. quercifolia* Klotsch, *C. ovalis* R. Br.

Gerascanthus somaliensis (Baker) Borhidi comb. nova - E. Afr.

- Basionym: *Cordia somaliensis* Baker Bull. Misc. Inf. Kew Bull.
1894: 28.

Gerascanthus suaveolens (Blume) Borhidi comb. nova - Java

- Basionym: *Cordia suaveolens* Blume Bijdr. 843.

Gerascanthus subpubescens (Decne) Borhidi comb. nova - Timor Isl.

- Basionym: *Cordia subpubescens* Decne Herb. Timor 67.

Gerascanthus trichostemon (DC.) Borhidi comb. nova - Timor Isl.

- Basionym: *Cordia trichostemon* DC. Prodr. 9:482. 1845.

Gerascanthus uncinulatus (DeWild) Borhidi comb. nova - Congo Belg.

- Basionym: *Cordia uncinulata* DeWild Rev. Zool. Afr. 9. Suppl. Bot.
89. 1921.

Gerascanthus venosus (Hemsl.) Borhidi comb. nova - China

- Basionym: *Cordia venosa* Hemsl. J. Linn. Soc. 26:143. 1890.

Gerascanthus vestitus (Hook. f. ex Thoms.) Borhidi comb. nova - India

- Basionym: *Cordia vestita* Hook. f. ex Thoms. J. Linn. Soc. 2:128.
1858.

According to our studies the following further species show calyptra-like opening of the calyx: *Cordia dodecandra* DC., *Cordia ecalyculata* Vell., *Cordia eriostigma* Pittier, *Cordia lutea* Lam. - *C. rotundifolia* Ruiz et Pav., *Cordia microcarpa* Killip, *Cordia silvestris* Fresen, taxa of very different systematic relations within the genus *Gerascanthus*. Motivated by these observations we did not maintain any systematic unit based on this feature.

ACKNOWLEDGEMENTS

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REFERENCES

- Britton, N.L., Millspaugh, C.F. (1925): Scientific Survey of Porto Rico and the Virgin Islands. New York Acad. Sci. 6:122-128.
- Browne, P. (1756): The Civil and Natural History of Jamaica. London.
- Candolle, A.P. de (1845): Prodromus Systematis naturalis Regni Vegetabilis sive enumeratio contracta etc. Paris 9:467-502.

- Desvaux, N.A. (1808): Mémoire sur le genre Varronia. - J. Bot. 1. Paris.
- Endlicher, S. (1836-1840): Genera Plantarum Secundum Ordines Naturales Disposita. Vindobonae.
- Friesen, F.C.V. (1933): Les caractères essentiels de la famille des Sebestenaceae et revision du genre Varronia. Bull. Soc. Bot. Genève, 24:117-201.
- Gürke, M. (1893): Borraginaceae. In: Engler Natürliche Pflanzenfamilien IV/3. 81-86.
- Johnston, I.M. (1930): Studies in the Borraginaceae VIII. Contr. Gray Herb. Ser. 92:1-64. Cambridge, Mass.
- Johnston, I.M. (1940): Studies in Borraginaceae XVII. Cordia sect. Varronia in Mexico and Central America. - J. Arn. Arb. 30:85-110.
- Johnston, I.M. (1940): Studies in the Borraginaceae XV. Notes on some American and Central American species of Cordia. - J. Arn. Arb. 21: 336-355.
- Johnston, I.M. (1949): Studies in the Borraginaceae XVIII. Borraginaceae of Southern West Indies. - J. Arn. Arb. 30:111-138.
- Linné, C. (1753): Species Plantarum, ed. 1. 140-190. Holmiae.
- Moncada, M., Herrera, P.O. (1988): La palinología del género Cordia (Angiospermae: Boraginaceae) en Cuba. - Acta Bot. Cub. 58:1-10.
- Nowicke, J.W., Ridgway, J.E. (1973): Pollen studies in the genus Cordia (Boraginaceae). Amer. J. Bot. 60:484-591.
- Palacios-Chavez, R., Quiroz-Garcia, D.L. (1985): Catálogo palinológico para la flora de Vera Cruz. Familia Boraginaceae, género Cordia. - Biotica 10:1-113.
- Stearn, W.T. (1971): Taxonomic and nomenclatural notes on Jamaican gamopetalous plants. J. Arn. Arb. 52:614-647.
- Taroda, N., Gibbs, P. (1986a): A revision of the Brazilian species of Cordia subgenus Varronia (Boraginaceae) Notes RSG. Edinburgh 44:105-140.
- Taroda, N., Gibbs, P. (1986b): Studies on the genus Cordia L. (Boraginaceae) in Brazil. 1. A new infrageneric classification and conspectus. Rev. Bras. Bot. 9:31-42.
- Warfa, A.M. (1988a): Cordia africana Lam. (Boraginaceae) the correct name for Bruce's Wanzey. Taxon 37:961-963.
- Warfa, A.M. (1988b): Cordia (Boraginaceae) in NE Tropical Africa and tropical Arabia. Acta Univ. Ups. Diss. Fac. Sci. 174:1-78.
- Warfa, A.M. (1989): The identity and distribution of Cordia obtusa (Boraginaceae). Nord. J. Bot. 8: 489-491.

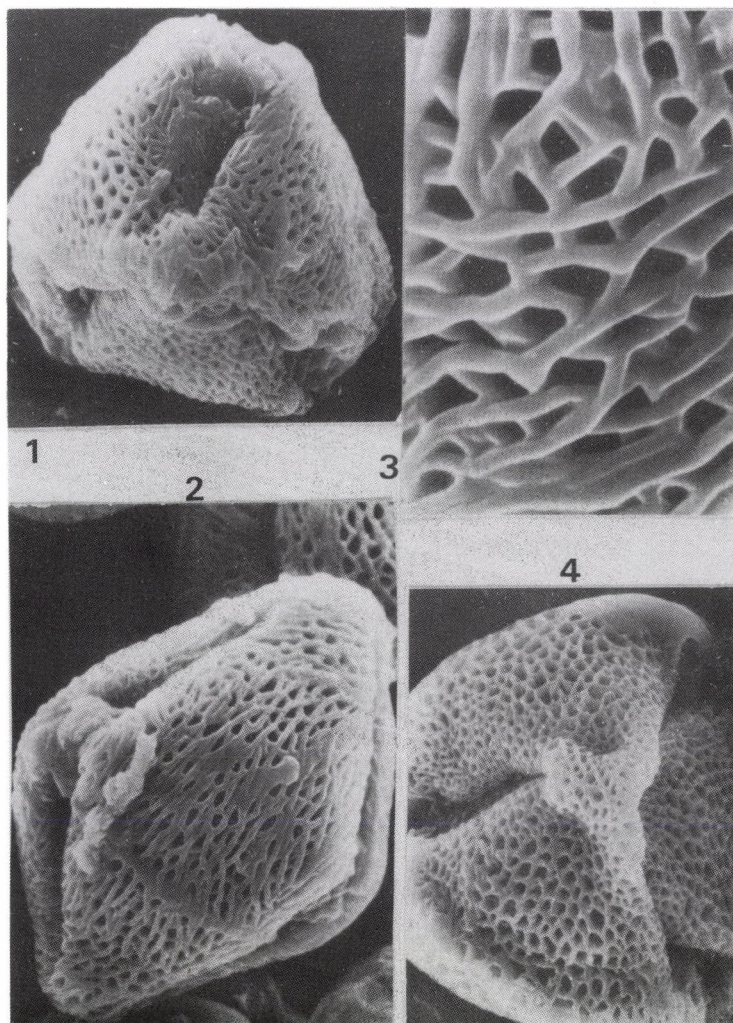


Plate I

Fig. 1. Pollen of Cordia boissieri, apical view, 2000 x

Fig. 2. Pollen of Cordia boissieri, lateral view, 2000 x

Fig. 3. Exine structure of Cordia boissieri, 7800 x

Fig. 4. Pollen of Cordia dodecandra, apical view, 2000 x

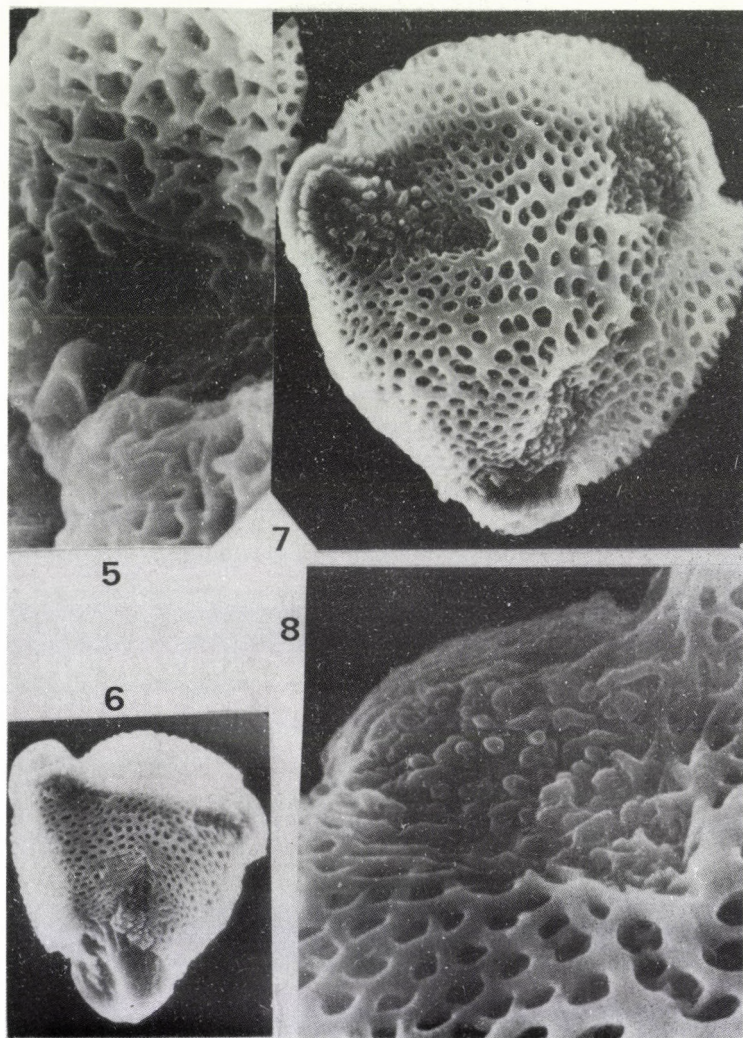


Plate II

Fig. 5. Colpus and porus of the pollen of Cordia dodecandra, 7800 x

Fig. 6. Pollen of Cordia ensifolia with macrocolpi, 1000 x

Fig. 7. Pollen of Cordia ensifolia, apical view, 2000 x

Fig. 8. Structure of exine and colpus of Cordia ensifolia, 7800 x

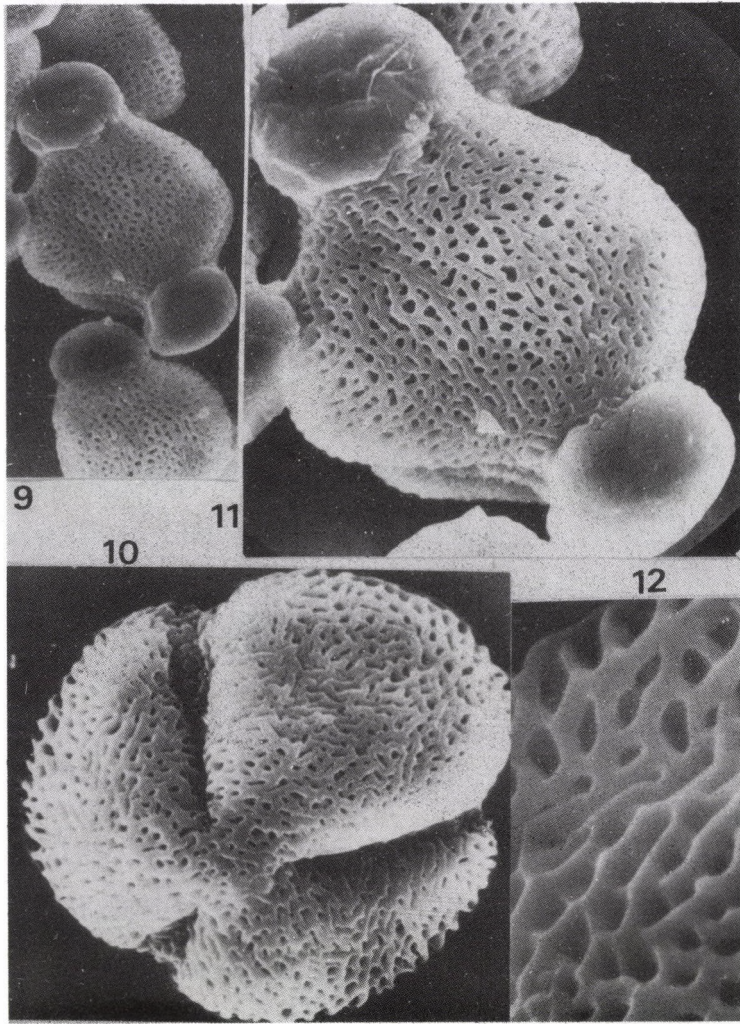


Plate III

Fig. 9. Cordia sebestena, pollen with macrocolpi, 1000 x

Fig. 10. Pollen of Cordia sebestena, apical view, 2000 x

Fig. 11. Pollen of Cordia sebestena with colpi, 2000 x

Fig. 12. Exine structure of the pollen of Cordia sebestena, 7800 x

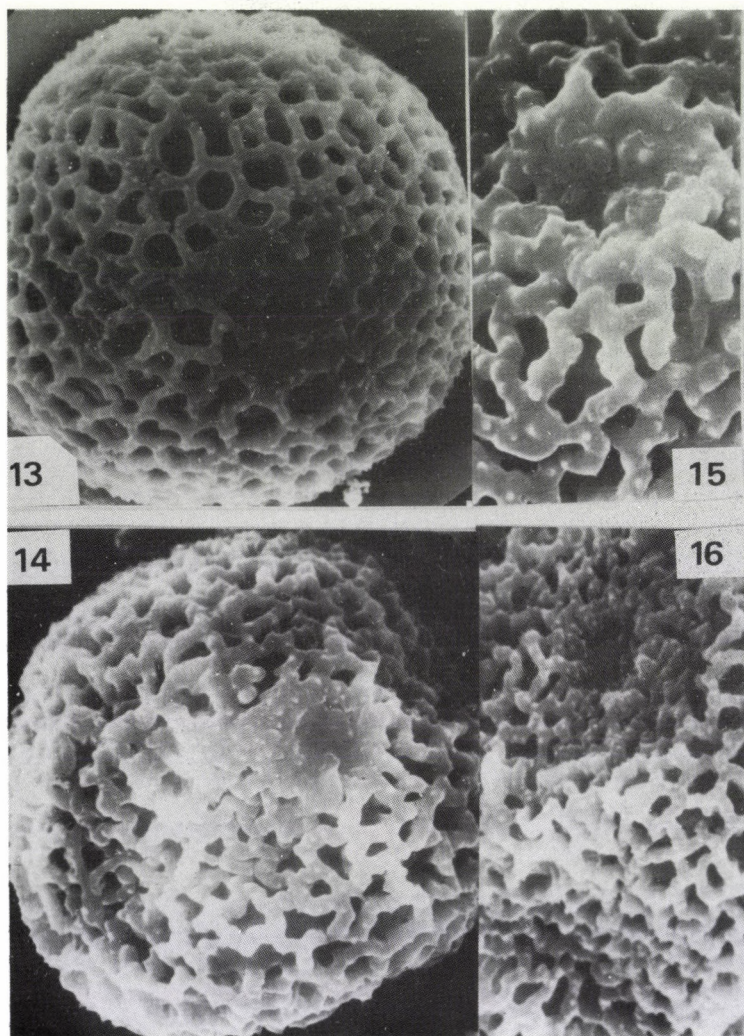


Plate IV

Fig. 13. Pollen of Varronia acuta, 2000 x

Fig. 14. Pollen of Varronia anderssonii with porus, 2000 x

Fig. 15. Exine structure of Varronia anderssonii, 7800 x

Fig. 16. Pollen of Varronia anisodonta, 2000 x

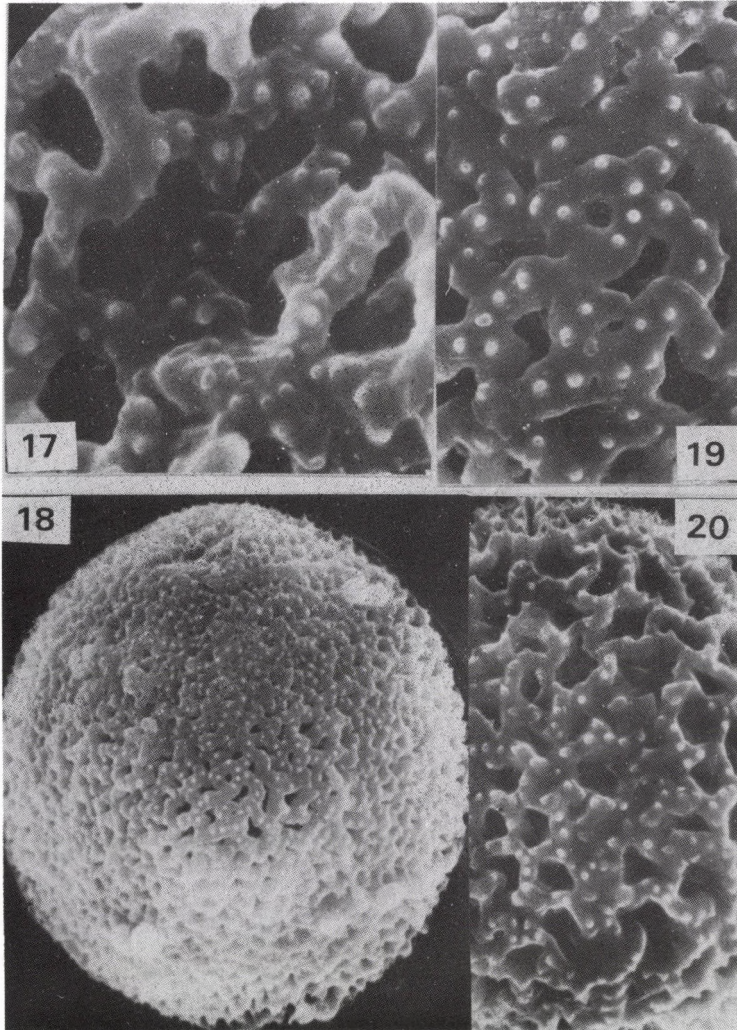


Plate V

Fig. 17. Pollen of Varronia anisodonta, exine structure, 7800 x

Fig. 18. Pollen of Varronia cephalocarpa, 2000 x

Fig. 19. Exine structure of Varronia cephalocarpa, 7800 x

Fig. 20. Exine structure of Varronia chabrensis, 3000 x

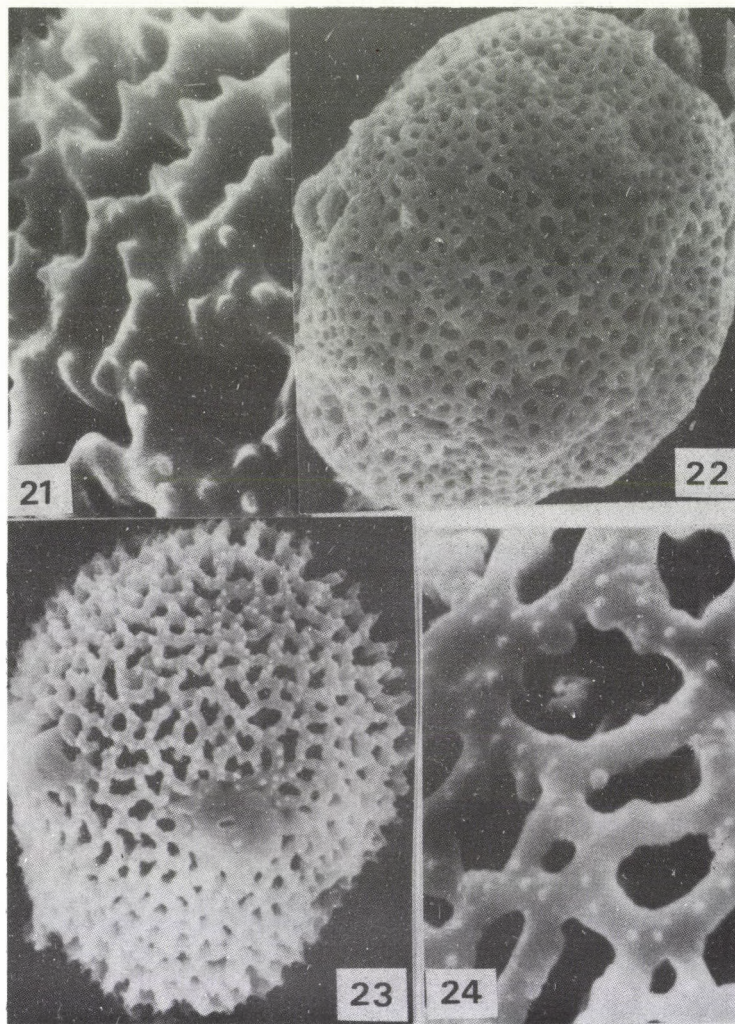


Plate VI

Fig. 21. Pollen of Varronia chabrensis, 7800 x

Fig. 22. Pollen of Varronia lamprophylla, 2000 x

Fig. 23. Pollen of Varronia macrocephala, 1500 x

Fig. 24. Exine structure of Varronia macrocephala, 7800 x

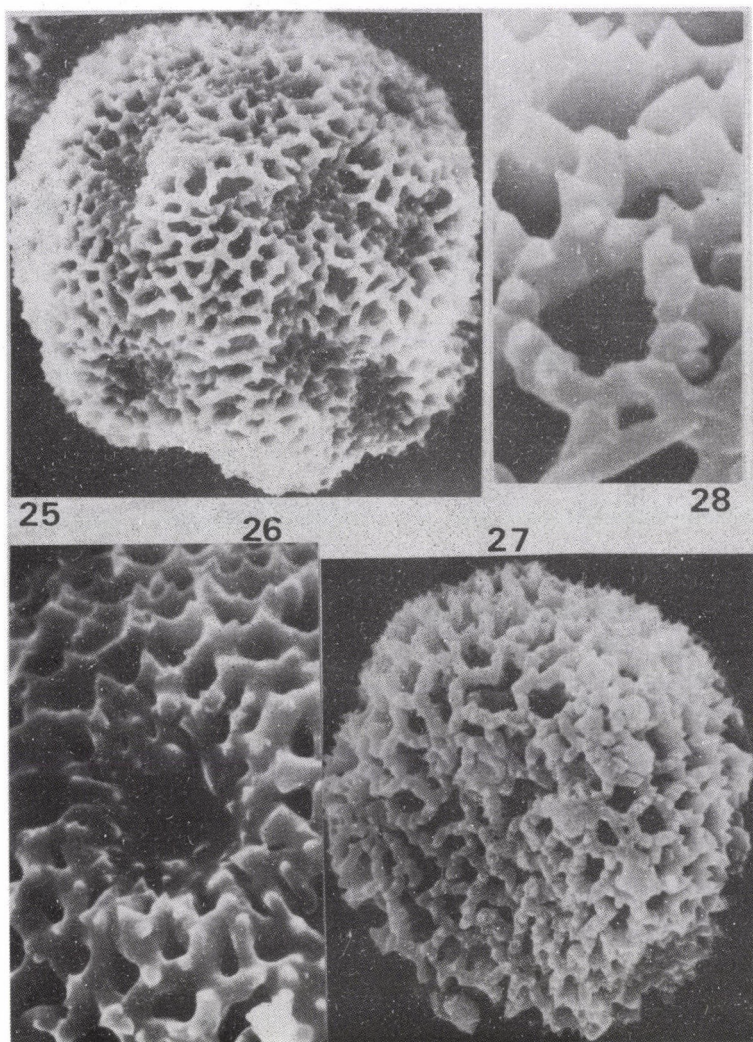


Plate VII

Fig. 25. Pentoporate pollen of Varronia serrata, 2000 x

Fig. 26. Porus and exine of Varronia serrata, 4000 x

Fig. 27. Pollen of Varronia nesophila, 2000 x

Fig. 28. Exine structure of Varronia nesophila, 7800 x

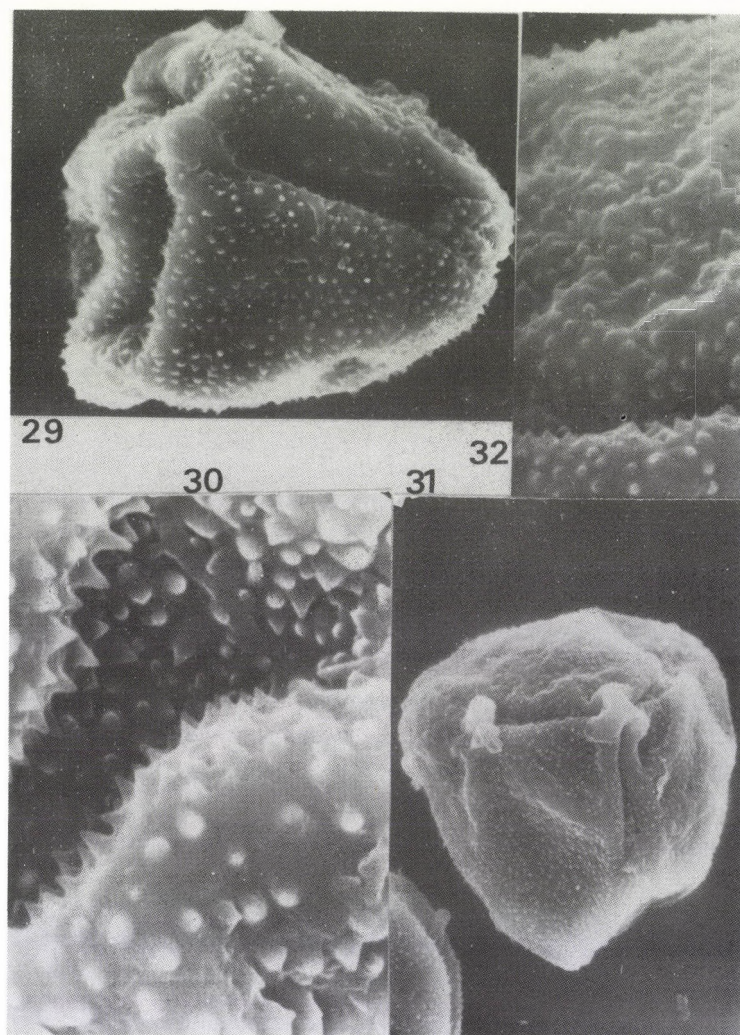


Plate VIII

Fig. 29. Pollen of Gerascanthus africanus, apical view, 2000 x

Fig. 30. Exine structure of Gerascanthus africanus, 7800 x

Fig. 31. Pollen of Gerascanthus albus, 2000 x

Fig. 32. Exine structure of Gerascanthus albus, 7800 x

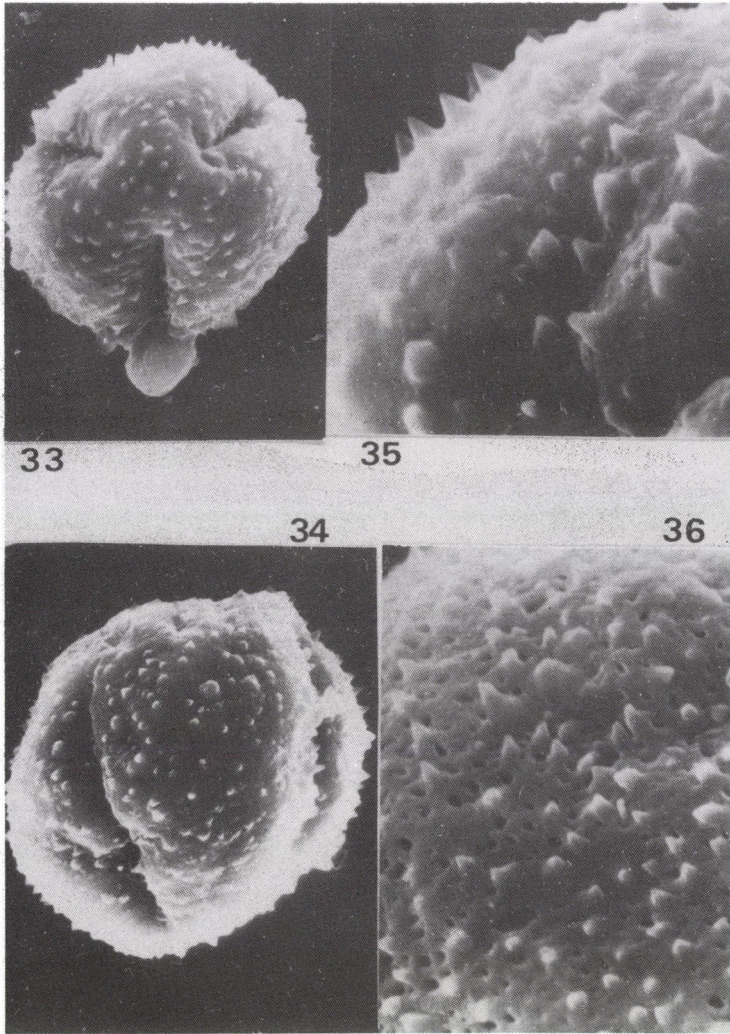


Plate IX

Fig. 33. Pollen of Gerascanthus alliiodorus, apical view, 2000 x

Fig. 34. Pollen of Gerascanthus alliiodorus, lateral view, 2000 x

Fig. 35. Exine structure of Gerascanthus alliiodorus, 7800 x

Fig. 36. Exine structure of Gerascanthus asperus, 7800 x

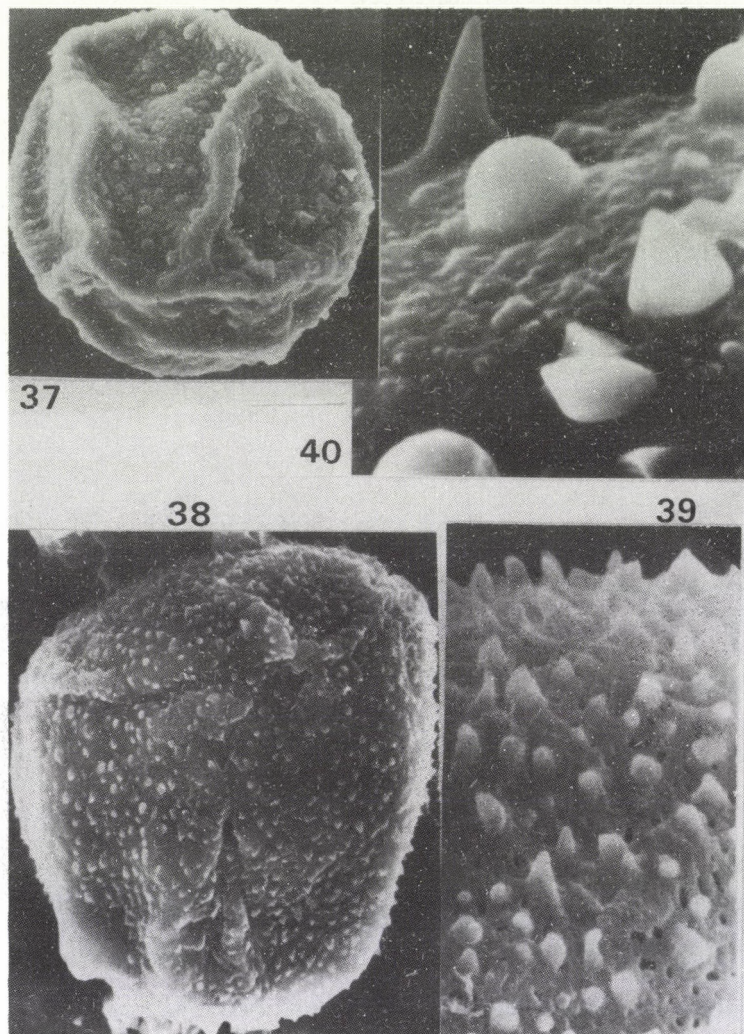


Plate X

Fig. 37. Pollen of *Gerascanthus aurantiacus*, 2000 x

Fig. 38. Pollen of *Gerascanthus caffra*, apical view, 2000 x

Fig. 39. Exine structure of *Gerascanthus caffra*, 7800 x

Fig. 40. Exine structure of *Gerascanthus collococcus*, 7800 x

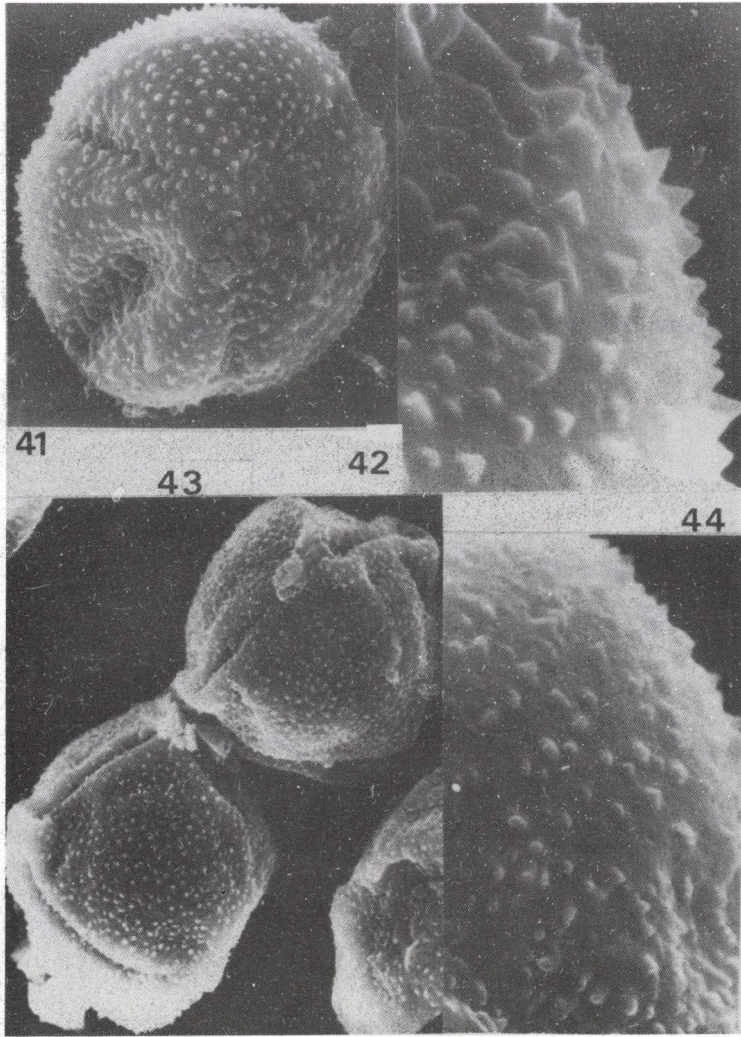


Plate XI

Fig. 41. Pollen of Gerascanthus millenii, 2000 x

Fig. 42. Exine structure of Gerascanthus millenii, 7800 x

Fig. 43. Pollen of Gerascanthus decandrus, 2000 x

Fig. 44. Exine structure of Gerascanthus decandrus, 7800 x

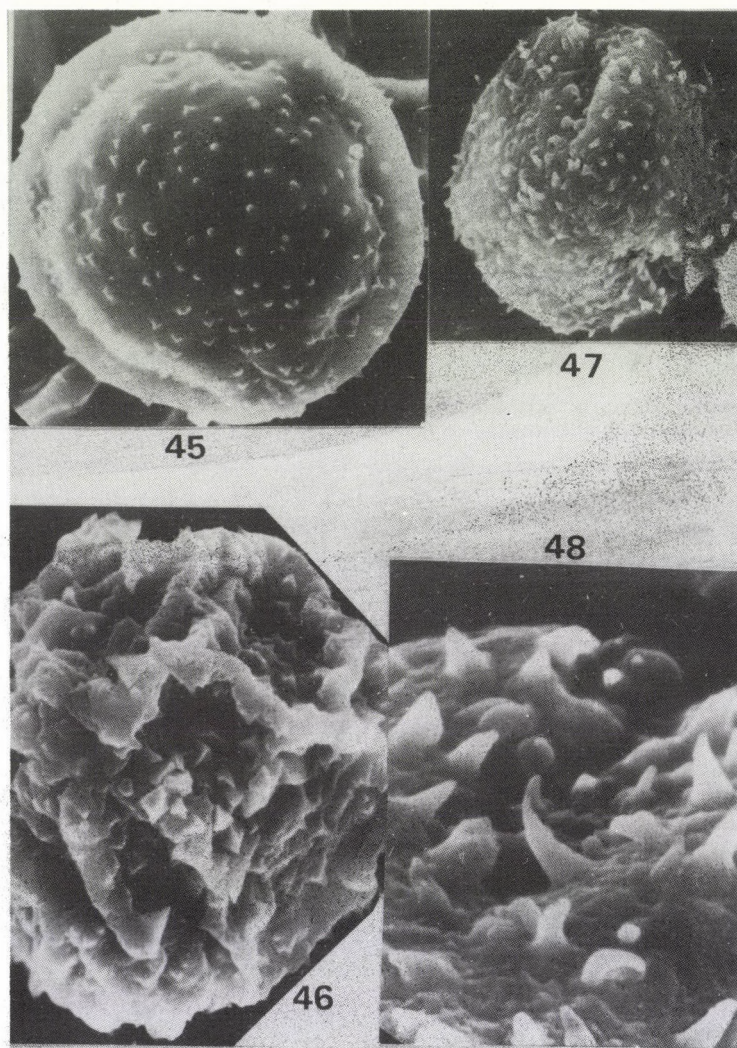


Plate XII

Fig. 45. Pollen of Gerascanthus ellipticus, 2000 x

Fig. 46. Pollen of Gerascanthus eriostigma, 3000 x

Fig. 47. Pollen of Gerascanthus gerascanthoides, 2000 x

Fig. 48. Exine structure of Gerascanthus gerascanthoides, 7800 x

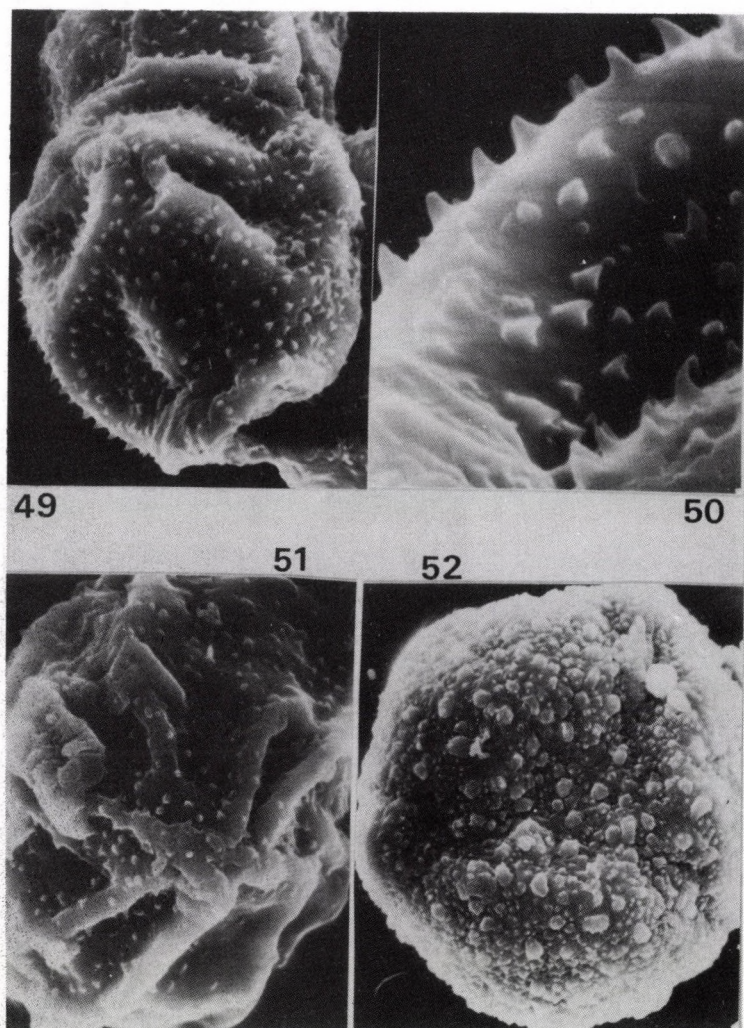


Plate XIII

Fig. 49. Pollen of Gerascanthus goetzei, 2000 x

Fig. 50. Exine of Gerascanthus goetzei, 7800 x

Fig. 51. Pollen of Gerascanthus griffithii, 2000 x

Fig. 52. Pollen of Gerascanthus luteus, 2000 x

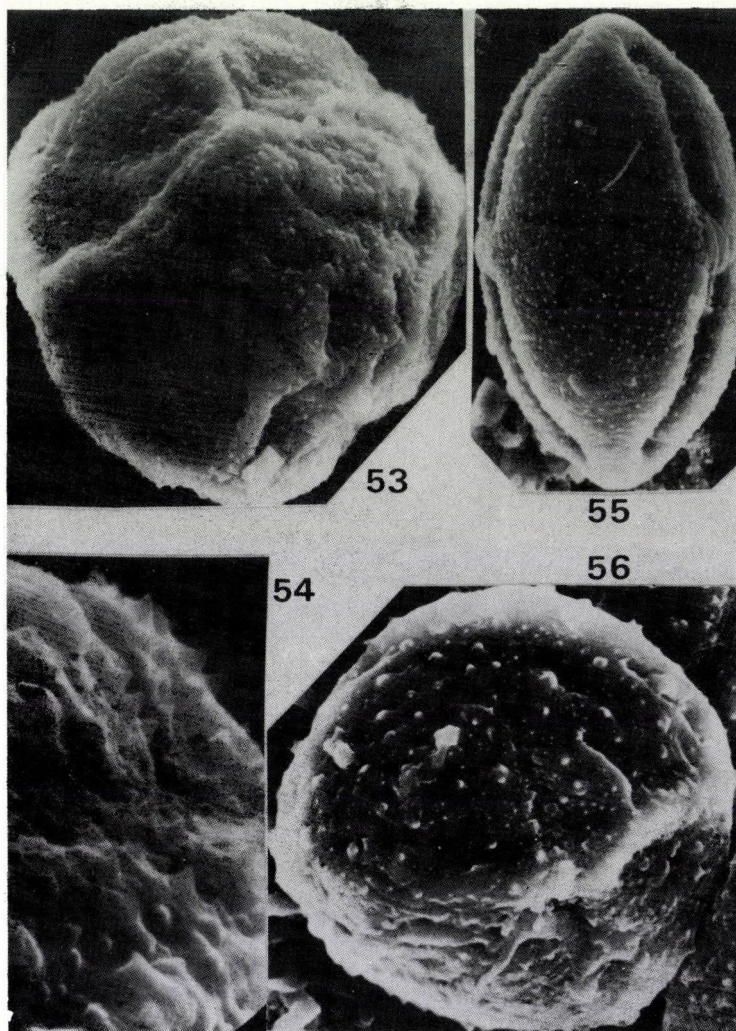


Plate XIV

Fig. 53. Pollen of Gerascanthus myxus, 2000 x

Fig. 54. Exine structure of Gerascanthus myxus, 7800 x

Fig. 55. Pollen of Gerascanthus megalanthus, 2000 x

Fig. 56. Pollen of Gerascanthus nodosus, 2000 x

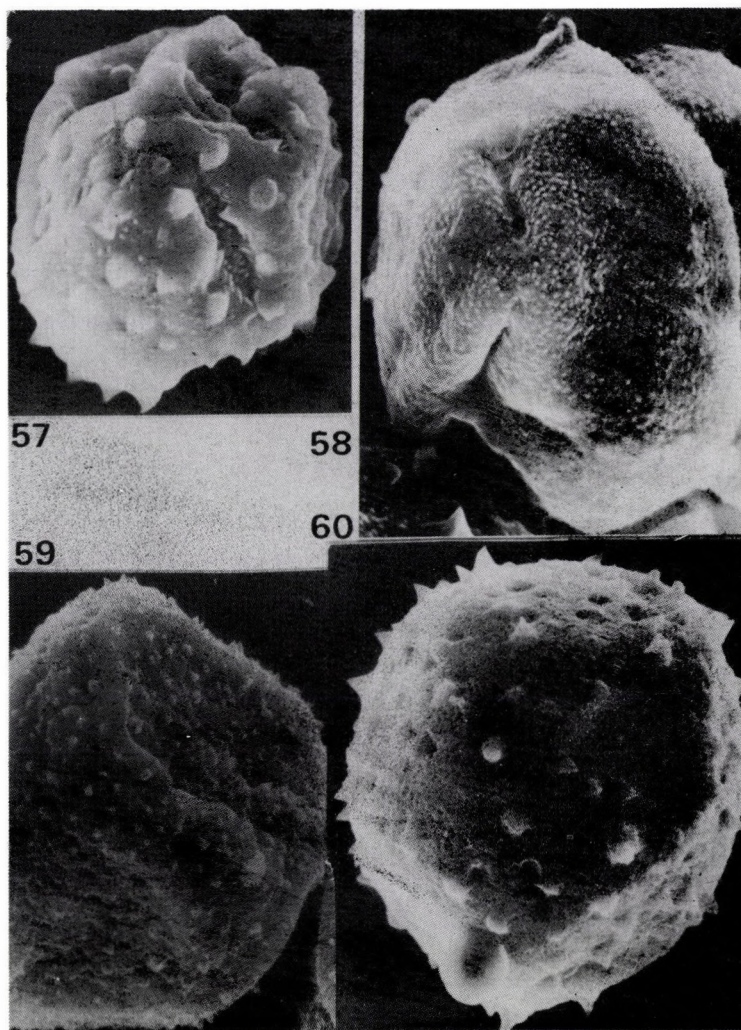


Plate XV

Fig. 57. Pollen of Gerascanthus microcarpus, 2000 x

Fig. 58. Pollen of Gerascanthus obovatus, 2000 x

Fig. 59. Pollen of Gerascanthus sellowianus, 2000 x

Fig. 60. Pollen of Gerascanthus silvestris, 2000 x

BOOK REVIEWS

edited by Z. Szűcs

TRABALKA, J.R. — REICHLÉ, D.E. (ed.): The Changing Carbon Cycle. A Global Analysis. Springer, New York — Berlin — London, 1986, 592 pp.

The potential importance of the radiatively active gases in the atmosphere in maintaining the heat balance and spectral properties of the earth has been recognized for nearly a century. It is now realized that the earth's atmosphere has evolved over billions of years as a result of natural biogeochemical processes. The influence of the atmosphere of earth's biological evolution (and vice versa) through geologic time has become a basic scientific premise.

We now appreciate that living organisms, and the life processes, have had a marked effect on the development of the earth's atmosphere, producing a closely coupled system whereby the crucial chemical and radiative environment necessary for this planet's habitability is maintained.

In the last decades there has been a growing sensitivity and concern of the impact of human activities on environment as the global industrialization was causing exponential growth in energy production and consumption. Historically, much of the world's energy production has been derived from the combustion of fossil fuels, and little change in this pattern is foreseen before the end of this century. Farsighted scientists have raised questions about the potential consequences of the annual release of several billion metric tons of CO_2 from fossil combustion. Since the well-documented measurements from the Mauna Loa Observatory, Hawaii (beginning in the late 50s) have become available, a convincing, steady rise in atmospheric CO_2 concentration as a parallel phenomenon to the fossil fuel consumption has become an accepted fact. Both processes have an accelerating (exponential) character.

The concerned USA agencies, such as National Science Foundation, US Department of Energy, Oak Ridge National Laboratory, Electric Power Research Institute and National Oceanic and Atmospheric Adm. cognizant their collective responsibility to future generations have been spent 9 years and about 100 million \$ directly on the cooperative study into the causes, effects, and potential impacts of increased CO_2 concentration in the atmosphere. The Department of Energy is scheduled to summarize the scientific understanding of CO_2 -climate change issue, including the global carbon cycle, in a series of technical reviews to be published from 1985. As a preparation of the review status, the Sixth Annual Oak Ridge National Laboratory Life Sciences Symposium was devoted to the topic of "The Global Carbon Cycle: Analysis of the Natural Cycle and Implications Anthropogenic Alterations for the Next Century". The world's experts from internationally renowned institutions were asked to critically review the key issues. The Symposium was held in November, 1983, in Knoxville, Tennessee, USA.

This volume is the result of the presentations at this Symposium, carefully selected and critically reviewed to represent a summary of our understanding of some of the most important scientific issues concerning to the global carbon cycle.

The first five chapters discuss the atmospheric concentration of CO_2 , beginning with the most recent patterns of increases and progressively backward in time.

Four subsequent chapters focus on a central dilemma of current scientific investigation — that of using sophisticated analytical techniques and interpreting ratios of carbon isotopes in tree rings and geologic media

laid down over past centuries to both estimate historic atmospheric concentrations of CO_2 , identify sources both fossil and biological.

The atmosphere is only one of the three major global reservoirs of carbon. The second big reservoir, the terrestrial biota and soils as the biologically most active living part of the whole system, is discussed in the next four chapters. Clearing land of vegetation (mostly forests), with its resulting release of CO_2 through burning and decomposition, is a major perturbation of the natural gaseous exchange of photosynthesis and respiration between land and atmosphere.

According to the estimations, the clearing the land for permanent agriculture was responsible for 60–90% of the net release of carbon into atmosphere between 1860 and 1980. Shifting cultivation accounted for most of the remainder. The replacement of traditional shifting cultivation with a permanent form of subsistence agriculture in recent years has resulted in an expansion of these degraded lands.

Large areas formerly forested are no longer able to support either subsistence crops or the regrowth of forests. Most probably the vast territories of Southeast Asia are the result of man's overuse of forests.

There are very significant findings in one of the chapters dealing with the changes in soil carbon storage in relation to clearing of vegetation, agricultural use, erosion, reforestation etc. The general trend of soil carbon (organic matter) content's decrease is about 30% over a period of 20–50 years. Losses in the surface layers are often more than 30%. The major loss of soil carbon occurs in the first 20 years after land-use conversion to agriculture from forest, and is associated with an increased release of CO_2 from soils to the atmosphere.

One of the most exciting chapter is about the use of remote sensing in monitoring of vegetation cover in continental and global scale. There were even magnitudinal differences between the previous estimations, especially that of the tropical forest clearing. Now, based on LANDSAT satellites and using a specially vegetation-oriented spectral bandwidths, we are able gain accurate pictures from the whole globe on a nearly daily basis. Thus it is possible to overcome cloud cover, atmospheric effects and other hindrances, too. At a resolution scale of 1 km, one can easily detect ongoing process of forest clearing very accurately. This chapter gives excellent pictures and detailed analysis of them from the Amazon Basin, Brasil, as an example of tropical deforestation monitoring, and gives a proof of the previous hypothesis of accelerating rate of forest clearing in this area. An other very valuable application of this technique is the continental scale land cover classification. This is demonstrated by the example of Africa's vegetation. Based on the difference of intensity of "greenness" among the vegetation types and zones, a fresh and up-to-date vegetation map is presented here from Africa. This pictures can show clearly also the seasonal changes of chlorofil content of vegetation.

The next five chapters are devoted to carbon cycles in the ocean.

How all these can be synthesized, interpreted and used to address the central issue of the volume – that of the role of anthropogenic CO_2 emissions to the atmosphere in changing the global carbon cycle – is treated in the last section. These nine chapters are centered around the modelling problems of the global carbon cycle, especially for using these models for forecast. First the general requirements for a satisfactory model representation are set forth. Then it is discussed, how such models can be calibrated and validated, and how the seasonal and geographical patterns of atmospheric CO_2 provide information on current global carbon balance. Then globally averaged carbon cycle models are used in conjunction with model projections of fuel usage and CO_2 emissions to estimate the likely bounds

of future atmospheric CO₂ levels and the potential confounding effects of other radiatively active gases. These chapters raise as many questions as they answer but are invaluable in assessing the implications of our present knowledge and in setting the stage for future endeavors.

The whole volume is well-documented, clearly written and highly informative. It gives an excellent and almost totally comprehensive cross section of the state of art. It will most certainly be welcomed by ecologists, meteorologists, soil scientists, geologists, global modelers, even economists; both professionals and interested students.

Z. SZÖCS

BEWLEY, J. — BLACK, M.: *Seeds. Physiology of Development and Germination*. Plenum Press, New York and London 1985, 367 pp.

Several years ago the same authors have already published an important two volumed monography on this field (*The Physiology and Biochemistry of Seeds in Relation to Germination*. Springer, Berlin etc., 1978 and 1982), but their present book — as they expound in the preface — has other goals: it is like a textbook of high level, intended for university teachers and students. To these persons the book can be recommended without reserves, because it succeeds very well in giving a short but modern picture (based on the literature in English up to 1982) of all the important chapters of seed biology, with due stress — though this is not expressed in the titel — also on its biochemical and cytological aspects. This completeness and broadness of the horizon are the greatest merits of the book, as shown by a simple enumeration of the chapters: 1. Seeds: Germination, Structure and Composition; 2. Seed Development and Maturation (also sources of assimilates, deposition of reserves, seed hormones and their roles); 3. Storage, Inhibition and Germination (with a detailed discussion on seed ageing and vitality); 4. Cellular Events during Germination and Seedling Growth (comprising also respiration, protein and nucleic acid syntheses); 5. Dormancy and the Control of Germination (with thorough subdivisions on internal, external and environmental factors as well as on the development of dormancy); 6. Some Ecophysiological Aspects of Germination; 7. Mobilization of Stored Seed Reserves (not only of carbohydrates, proteins and lipids, but also of stored phosphates); 8. Control of the Mobilization of Seed Reserves (of course with emphasis on cereals but dicotyledons are also discussed); 9. Seeds and Germination: Some Agricultural and Industrial Aspects (with interesting subdivisions on malting, preharvest sprouting, genetic conservation as well as — perhaps in a too short form — presowing osmotic and water treatments).

The book is not without some minor flaws. The list of the omitted concepts is laudably short: rudimentary embryos as a dormancy mechanism, and treatments to abolish coat imposed dormancy are missing. Vigor is mentioned but not defined. (It is no fault that emergence has been deliberately left out.) Dormancy forms would need a clearer definition and a more complete classification. What is told on dormancy on p. 2, seems to exclude its coat imposed forms. Relative dormancy is absent in the classification of dormancy categories on p. 177, and, when mentioned later (p. 191) it is not separated from quiescence logically. According to p. 193, primary and secondary dormancy may not be fundamentally different, but this is contradicted by the preceeding statement (*ibidem*) that different factors are required to break these two forms. The view (p. 192) that relative dormancy is simply a consequence of increased membrane fluidity is not entirely convincing in its actual formulation.

Sometimes a better coordination of the chapters would have been useful. E.g. free radical processes as ageing mechanisms deteriorating membranes, proteins, nucleic acids etc. are aptly presented on p. 111, but when speaking of oxygen toxicity (p. 97) and of indigenous mutagens as possible factors in seed ageing (p. 109) they are overlooked. From what is said on p. 93, it may be deduced that a great water content is always harmful for stored seed, but this is in conflict with p. 110, according to which some dormant seeds are best preserved in the fully imbibed state. Generally a greater number of cross-references would have been useful.

The complete omission of literature references and (with perhaps two exceptions) of author names from the text (but not from the figure captions) is debatable as it renders the work of the attentive reader more difficult.

Finally a remark on the nomenclature. The expression "recalcitrant seeds" — i.e. "unorthodox", drying intolerant ones — seems misleading. It would be best to drop it.

These remarks do not detract anything of the merits of this very valuable book. Manly chapters of it can be read with profit even by people more advanced in this field than those whom it is originally written for.

L. PÓLYA

DIGBY, P.G.N. — KEMPTON, R.A.: *Multivariate Analysis of Ecological Communities*. Chapman and Hall, London. 1987. 206 pp.

The past few years have witnessed a proliferation of books dealing with the application of multivariate methods to community ecology. These books vary in methodological depth and ecological relevance; some emphasize algorithmic details while others try to avoid mathematical formalism completely. This book finds a good balance between statistics and ecology: multivariate methods are described using many terms of matrix algebra and case studies illustrate the usefulness of most techniques discussed. The price is high for some readers, however. Some parts of the text are difficult to follow without a thorough understanding of matrix operations, so I do not share the view expressed in the back cover that the book is accessible to those with little mathematical expertise.

A short discussion of data types, standardization methods and measures of association introduces the reader into multivariate statistics. Data types are loosely defined as being binary, qualitative, and quantitative. Unfortunately, this categorization is vague; instead, it would have been more accurate to rely on scale types (nominal, ordinal, etc.). Metric and Euclidean properties of coefficients are discussed in some detail, following a recent study by Gower and Legendre, but some measures often used in community studies (e.g., chord distance, angular separation, etc.) are neglected. This is unfortunate, for example, in view of a recent comparison of ordination methods which points to the superiority of chord distance in many scaling problems. Some inconsistency of the text is obvious because the book does mention the binary variant, i.e., the Ochiai coefficient, of this measure. Further shortcoming is that the authors fail to orientate the general user about the relative merits and disadvantages of distance measures.

The next chapter is a useful summarization of methods for the visual display of data. Chapter 3 is devoted to the ordination methods, including direct gradient analysis, principal components analysis, principal coordinates analysis, correspondence analysis and canonical variate analysis. Two alternative ways of the derivation of principal components are described

briefly. A detailed computational example would have been more helpful for the average reader to understand what is going on in PCA (the authors' attempt to introduce a new acronym, PCP, for this method just increases the chance for terminological confusion). Ecologists will be very much interested in the discussion of biplots; examples demonstrate how to display quadrat and species scores simultaneously based on PCA results. This is a very useful section of the book.

The description of other ordination methods is even more concise than that of PCA. Previous knowledge of these procedures is usually necessary to follow the derivations. Many things become clear later in the text, for example, when the relationships between principal coordinates analysis and other methods are revealed. The section on metric ordinations is concluded by discussing the horseshoe (arch) effect and its treatment. Note that Williamson's technique for the removal of this effect is not restricted to presence/absence data as stated. Compared to the metric methods, non-metric scaling is superficially treated and no (!) references are given.

The topic of comparing ordinations received a separate chapter in the book. Generalized and multiple Procrustes analyses are described in detail. These procedures are useful if raw coordinates are available; an alternative way for comparison is offered by INDSCAL method of CARROLL and CHANG, if ordinations are described in terms of interpoint distances, but this method is not mentioned.

Chapter 5 is devoted to classification. Selected procedures of clustering are introduced. However, these are not necessarily the most frequented ones in community analysis. The case studies illustrate various ways of displaying classifications and show superposition of clusters onto ordination scattergrams as a useful means of data exploration. Contrary to the case of ordinations, the comparison of classifications is very short and thus provides limited information about the subject.

The most unique section of the book deals with the analysis of asymmetric matrices. The examples include analysis of heathland succession and competition of grassland species. Plant ecologists will most certainly find this chapter very stimulating.

Although I focused on some problems in the book, it appears valuable for everybody interested in multivariate techniques and their application to community studies. Whereas some sections may be criticized on the grounds that the authors' subjective feelings determined selection of methods, the book as a whole is a good summarization of information for those already familiar with the fundamentals of multivariate statistics and may be used as a reference guide.

J. PODANI

KRAMMER, K. — LANGE-BERTALOT, H.: *Bacillariophyceae* 1. Teil: *Naviculaceae*. In: H. Ettl, J. Gerloff, H. Heynig und D. Mollenhauer (eds), *Süßwasserflora von Mitteleuropa*. Band 2. G. Fischer Verlag, Jena 1986, 876 pp.

The most recent volume of the series "*Süßwasserflora von Mitteleuropa*" was expected to appear perhaps more eagerly than any other algological identification book. The first part of the monograph on *Bacillariophyceae* is written by K. KRAMER and H. LANGE-BERTALOT, noted experts of diatoms, and introduces the family of *Naviculaceae*.

After the Preface, the objectives and the main principles followed during the preparation of the book are summarized in 13 points. Based on the identification key to the 20 classes of algae, which is compiled ac-

cording to a new approach published in 1984, the Bacillariophyceae may be unambiguously distinguished from the other algae.

The Introduction and general part, which is longer and more detailed than usual in the former books of the series, fall into ten subtitles. The terminological part, which includes a glossary of important terms, is especially useful. This is the first identification book which follows closely the terminology recommended by international standards. In addition to discussing the terminology of the frustule, the authors present drawings and light- and electronmicroscopic photographs, which complement the text. The authors warn that the features may vary with species, and a given feature of character may be different in the inner and outer part of valve face. This is illustrated by many examples (184 micrographs and figures on 25 plates). As an appendix of the glossary, the English, French and Latin versions of the German morphological terms are listed.

Then, the detailed morphological description of the frustule follows with ample references. The asexual organelles, the morphogenesis of the cell wall, and the special locomotion of diatoms are discussed.

An important subchapter is devoted to the distribution and ecology of diatoms. Within the latter topic, we find separate subtitles on the pH conditions, electric conductivity, oxygene saturation, tolerance against sewage water and, within the latter, on the role of saprobiological indication. We are also informed on the applicability of diatoms to the measurement of saprobity.

The next methodical part describes methods of collecting, preserving and cleaning diatom frustules, both recent and fossil materials. As the final part of the introductory section, embedding materials used in preparing permanent slides, preparation techniques in EM and LM studies, and the LM and EM studies themselves are described.

In the next section a special part includes the principles of diatom systematics, the taxonomy of diatom genera and the detailed description of the Naviculaceae family. Following the general characterization of the family, an identification key to the 22 genera is the starting point to the identification of a Naviculaceae species.

In case of the Navicula genus, the authors do not follow the tradition of organizing the key according to subgenera and sections. Instead, a more complex and less easily comprehensible grouping is presented, which guarantees a more correct identification. The main groups from A to N are the keygroups, which sometimes correspond to the former subgenera or species groups. In the last key group we find subgroups as well. For each key group a precise identification key is given for the particular species. One should not be surprised that many species occur in several keys; this is a natural consequence of the high morphological variability of diatoms.

The keys are followed by the detailed description of species, references to figures, distributional data, ecological characteristics, with many references to the literature.

The numbers of species in the genera are as follows:

<u>Navicula</u>	247	<u>Amphora</u>	19
<u>Stauroneis</u>	29	<u>Gomphonema</u>	27
<u>Anomoeneis</u>	8	<u>Gomphoneis</u>	1
<u>Frustulia</u>	5	<u>Didymosphenia</u>	1
<u>Amphipectus</u>	4	<u>Rhoicosphenia</u>	1
<u>Neidium</u>	29	<u>Caloneis</u>	24
<u>Scoliopleura</u>	1	<u>Pinnularia</u>	55
<u>Diploneis</u>	20	<u>Mastogloia</u>	6
<u>Pleurosigma</u>	3	<u>Diatomella</u>	1
<u>Gyrosigma</u>	12	<u>Oestrupia</u>	2
<u>Cymbella</u>	74	<u>Entomoneis</u>	4

It was a good idea to break the tradition by replacing drawings with LM, TEM and SEM micrographs. These micrographs, whose quality is excellent in most cases, facilitate much better the identification of diatoms than drawings. On the average, 5 figures illustrate each of the 572 species (disregarding the varieties). The printing of figures as well as the text is of very high quality, just as in the earlier volumes of this series.

There is only one critical shortcoming in the book. References are included only in the text, the bibliography is missing from this volume. Although it seems logical to give only one bibliography for a three-volume set in the last volume, if they appear separately this is still a wrong decision.

The book by KRAMMER and BERTALOT will certainly be a leading monograph in diatom research, such as the corresponding volume in the old PASCHER series. We are looking forward to the other two volumes to appear. This volume is warmly recommended to diatomologists and algologists, and also to taxonomists, hydrobiologists and all other biologists working in the field of hydrology. The book may be used successfully as a textbook in university courses, and elsewhere if correct identification of diatoms is required.

K.T. KISS

FOGED, N.: *Diatoms in Gambia*. 154 pp., 25 plates. — *Diatoms in the Volo Bay, Greece*. 68 pp., 13 plates. — *Bibliotheca Diatomologica* 12. J. Cramer, Berlin — Stuttgart, 1986.

This is the fourth volume written by N. FOGED for the series *Bibliotheca Diatomologica*. The structure of the book follows that of FOGED's earlier works in this series.

The sections on the diatoms of Gambia and Volo Bay start with a short abstract, then follow the introduction, description of sample sites, detailed systematic part, comments, references and plates.

The first part reports on the study of 35 samples collected in Gambia and Senegal; 20 are proper littoral and at least 5 are proper freshwater samples. A total of 338 diatom taxa were identified, they belong to 71 genera. In the systematic part the genera, and within genera the species and lower taxa, are described in alphabetical order. For each taxon literature data are presented first for identification, and previous records are listed. Then, the samples are given in which the taxon was recorded. The serial number of sample follows so that the locality may be easily identified. If a photograph is included, references to the figure and morphometric characteristics are presented. Finally, remarks on the ecology and distribution of the taxon are given.

In summarizing the ecological studies, the author concludes that of the 338 diatom taxa 117 are polyhalobe, 55 are mesohalobe and 106 are oligohalobe.

This section is completed by 224 bibliographic items, and 300 micrographs showing 219 different taxa on 25 plates.

The second, and smaller part is an account on the diatoms of Volo Bay of the Aegean Sea. The results are based on 8 samples and are presented in a manner described above. 152 taxa from 36 genera are presented; 141 are mesohalobe and polyhalobe, 11 are oligohalobe. The number of bibliographic items is 45; the illustrative material contains 127 micrographs showing 113 taxa on 13 plates.

Two comments deserve mention here. It is unfortunate that no detailed morphological description is given for rarely discussed and taxonomically

problematic species (as done by ARCHIBALD in vol. 1 of the series). In addition to the excellent microscopic photographs, TEM and SEM micrographs would have improved greatly the value of the book. A comment by the author corroborates this statement: "no new species are described from the analysed material, even though it without doubt should be possible to demonstrate several, especially marine new taxa. But because most of them are very small, less than 10–20 μm , a reasonable description should demand a basis of REM photos, which I am not able to give".

Nevertheless, the richly illustrated, well-structured and highly informative book is recommended for all diatomologists, algologists, and hydrobiologists dealing with taxonomical and practical problems.

K.T. KISS

MANLY, B.F.J.: *Multivariate Statistical Methods. A Primer*. Chapman and Hall, London

There are dozens of books treating multivariate methods at an introductory level so the reviewer's main task is to examine whether this new book is essentially different from the others or simply a rephrasing of widely-known information. Another aspect to be considered is the suitability of the book for the target audience. The author's aim was to write a text for students who have previously taken a standard course on multivariate statistical methods, so this book is a natural generalization towards the multivariate problems. The link between univariate and multivariate tests is adequately founded in Chapter 3, although some methods (e.g., Levene's test, Van Valen's test), that are less known even for biometricians, should have received a bit more attention, especially as regards their limitations of applicability.

The discussion turns to the measurement of distances between individuals or between populations in Chapter 4. Euclidean distance, Penrose and Mahalanobis distances are selected from the multitude of available indices, and it is perhaps unfortunate to ignore coefficients for binary and mixed data. The discussion of Mantel test may contribute to the popularization of this useful Monte Carlo method of comparing two distance matrices.

Principal components analysis is introduced in algebraic terms in the next chapter. A geometric interpretation of the method would have been perhaps more illustrative for the novice. Also, limitations of PCA (e.g., dependence of linearity and the horseshoe effect) are not discussed. The differences between PCA and factor analysis are illuminated in Chapter 6. It is a pity that the PCA and factor analysis results for the same example (employment in European countries) are not contrasted. The next chapter discusses canonical discriminant functions.

Cluster analysis is treated very briefly in Chapter 8. The discussion is limited to a few algorithms of hierarchical clustering, whereas some problems of cluster analysis are mentioned. The author warns that data reduction by PCA prior to cluster analysis may be inappropriate. Canonical correlation analysis is introduced next, together with tests of significance and the interpretation of canonical variates. Multidimensional scaling is the topic of the next chapter. Although reference is made to TORGERSON, the pioneer of classical metric scaling methods, in fact a nonmetric multidimensional scaling technique is described only. Thus, the distinction between metric and nonmetric methods remains unclear for the reader. In the Epilogue the author has several useful comments for students who wish to analyze their own data.

The examples used in the text are mostly biological but the book is comprehensible for non-biologists as well. The author gives some references for further reading after each chapter, and some computational aspects of the procedures are also discussed. Limitations on the size of the book certainly caused some insufficiency in a few chapters. Nevertheless, the author was successful in collecting introductory material which is scattered in more advanced texts of multivariate statistics.

J. PODANI

REITZ, M.: Die Alge im System der Pflanzen. *Nanochlorum eucaryotum* — eine Alge mit minimalen eukaryotischen Kriterien. G. Fischer Verlag, Stuttgart, New York 1986, 273 pp., 68 figures

It is an interesting volume with a quite unusual title; 80% of the text deals with the systematics of algae whereas the rest is devoted to a detailed description of a single species.

The systematic part is divided into 15 chapters. First, a brief overview of the system of plants and the place of algae in this system are presented. In discussing the organization levels of algae, the monadoid, rhizopodal, capsal, coccal, trichal and siphonal structures are characterized. The subsequent chapters cover the morphology, physiology, life cycle, reproduction and genetics of algal cells. The molecular biology of plant cell, with emphasis on algae, the chromatin of algal cells and of higher eukaryotic organisms, the molecular biological processes involved in DNA replication, the molecular biological taxonomy of algae, praebiological evolution, the evolution of cell and the ecology of algae comprise the topic of separate chapters.

This short description of the contents illuminates the problems with which recent algal taxonomy is faced. To resolve the difficulties, the author suggests the more extensive application of molecular biological techniques, which appear suitable to clarify taxonomical questions. The results of molecular biological studies on algae necessitate that molecular biological criteria should be considered as integral part of algal taxonomy. The central role of algae in the evolution of life is best understood by knowledge of molecular biology.

As an example, *Nanochlorum eucaryotum* is examined in much detail in Chapter 16. This small organism of 1.5–2 μm diameter cannot be identified using the morphological characters of classical taxonomy. This alga possesses both prokaryote and eukaryote characteristics, so that only a molecular biological approach may be successful to find its place in the system of plants. The author presents a detailed description of the morphology, physiology, biochemistry and molecular biology, and the taxonomic position of this species.

The latter chapter is especially important so much the more because in the past ten years many publications were devoted to the pikoplankton, the small, photoautotrophic organisms living mostly in the sea, which probably play a more significant role in the nutrient and energy cycles of the water ecosystems than earlier thought. However, the taxonomic analysis of these species is still in its initial stage.

The structure of the book is clear, the text is concise. The book fills a gap in several respects by providing a good summary of the topic. Particularly useful are the excellent micrographs and EM photographs, which facilitate a thoroughful characterization of *Nanochlorum eucaryotum*.

The book is supplemented with a rich bibliography (771 items) and an

index. It is warmly recommended to algologists and taxonomists; and the book is indispensable in university courses.

K.T. KISS

CURL, E.A. — TRUELOVE, B.: *The Rhizosphere*. Advanced Series in Agricultural Sciences 15. Springer Verlag, Berlin, 1985, 288 pp., 57 figures

Authors of the book define their subject as a narrow zone of soil influenced by living roots by leakage or exudation of substances that affect microbial activity. Even this definition suggests a possibility for a multidisciplinary approach. The aim of the book is really exceptional: to discuss the topic in its full details, going through all the concerned disciplines from plant anatomy to microbiology.

The authors intended to provide an overlook from a rather practical than theoretical side, and give a huge and colourful set of experimental results. Focusing on the rhizosphere they widened their consideration to all the connectable biota: the plant itself, the affected members of microflora and fauna, the inhabitants of "free" nonrhizosphere soil. General point of view of the book is "everything is connected with everything", but in this case it's far beyond phrases. Chapters take one after the other the most important taxa and examine the other possible interactions among them on a very systematic way. We can find examples on almost any pair of interacting partners (Protozoa — Bacteria, Bacteria-Fungi etc.) even with a lot of redundancies, self repetitions. These obstinantly returning questions are most frequent in chapters concerning with pathology, which topic seems to be overdetalled.

On the contrary: some chapters (1st—introduction, 2nd—root morphology, structure and physiology) don't overtake the information content of a university text book.

Chapter 3 deals with root exudates and sloughed organic matter. This part is a valuable source of information about methods used in collection and analysis of exudates. A chronological table summarizes the most important experiments up to 1983, showing the test-plant, the collection procedure and the way of chemical analysis. Some experimental systems are described in detail. Detected substances are characterised qualitatively and quantitatively within the major groups of carbohydrates, amino acids, organic acids, lipids, growth factors, enzymes, miscellaneous compounds. Another question is localisation of exudate releasing sites along the root. Among contradictory data the importance of root tips and sites of the formation of lateral roots is sure — not only due to regular exudation but the presence of sloughed and damaged cells.

Intensity of exudation and spectrum of substances depends on plant species, developmental stage and environment (temperature, light, soil moisture, nutritional elements). Presence of microorganisms, plant injuring factors or foliar biocide sprays also modify the exudation. General experience is that stress factors on plants induce more exudate release.

In Chapter 4 rhizosphere populations are taken into consideration. Thank to the "rhizosphere effect", density of many populations increase with decreasing distance from the root. Does the rhizosphere harbour a special microflora and fauna? After some introduction to standard methods and inhabiting taxons the rhizosphere-influenced qualitative changes are detailed. Another pages deal with factors determining the actual density of a given type of microbes. The major groups of soil dwelling animals (Protozoa, Nematoda, Acari and Collembola) are examined by their feeding

habits and dwelling sites. Root exudates can stimulate the egg-hatching of some nematode species.

Chapter 5 is a collection of examples on growth-promoting and inhibiting microbial interactions.

As microbial populations respond to the plant's state, the plant itself may derive benefit from or suffer the consequences of microbial activities in its self-created root environment. This creation takes place through affecting nutrient availability and pathogen activity in the soil. Rhizosphere microorganisms are of basic importance in mineralization, nutrient immobilization, nitrogen fixation, mycorrhiza-formation etc. They also play a crucial role in disease control performing competition with or direct stasis against pathogens. So Chapter 6 and 7 concentrate on agricultural applications.

The last chapter (Current Trends and Projected Emphasis) deals with alternative ways of biological control, and shows the consequences of different soil treating techniques with their possible side effects. Fundamental principles in modeling the rhizosphere are also mentioned.

The biggest value of the book is the excellent and concise description of relevant experiments. This big collection of results (more than 700 references are cited) is treated on a systematic and very critical way expressing doubts and showing that theoretical controversies often originate from differences of methods used.

All the chapters are wholes in themselves. Most of them contain a good historical and methodological introduction and all the informations concerning to the title. So you needn't read the book from cover to cover — even if you want to avoid redundancies. But the book as a whole helps "to feel a little in the place of the plant".

B. OBORNY

PÓCS, T. — SIMON, T. — TUBA, Z. — PODANI, J. (eds): Proceedings of the IAB conference of Bryoecology (Symposia Biologica Hungarica no. 35) — Akadémiai Kiadó, Budapest 1987, 902 pp. (2 bands)

Probably no other field within botanical research has undergone such a rapid development in recent times, as that of the bryoecology. As a result of this rapid development and also due to an increased interest in cryptogams in general, quite a few information c.q. theories on structural and functional adaption of bryophytes to their environment have accumulated. It was the International Association of Bryologists (IAB) which raised the idea to organize a conference, which would exclusively deal with bryoecology (the word ecology used in its widest sense). This first world congress of bryoecology was held in Budapest and Vácrátót (Hungary), on August 5–10, 1985.

Now, with the long-awaited publication of volume 35 in the series *Symposia Biologica Hungarica*, entitled "Proceedings of the IAB conference of Bryoecology", the lectures presented during this conference have come available. All together this volume contains the papers of 72 (and not 78 as mentioned in the information on the cover!) lectures, subdivided into six chapters (analogous to the respective sessions of the conference): 1. Physiological ecology, 2. Reproduction and dispersal ecology, 3. Community ecology, 4. Population ecology, 5. Bryophytes in ecosystems, 6. Bryophytes as bioindicators. The opening and concluding remarks of one of the Godfathers of bryoecology, P.W. RICHARDS complete and accessible subject index is given.

Chapter 1, on physiological ecology (session convener M.C.F. Proctor), is certainly the most diffuse part of the book (as a direct consequence of the conference!). It contains papers on such different, and partly not eco-physiological, topics as for instance: moss gardening (ANDO), microclimatology (IWATSUKI and HATTORI), cryptogam succession in relation to soil pH (MÁZSA, KOVÁCS-LÁNG and SNAKIN) and photosynthesis (MASAROVICOVÁ and ELIÁS; BALÓ; TUBA). Moreover, ZIELINSKI's interesting paper on genetic variation in the liverwort genus *Pellia* would have fit, in my opinion, much better in the chapter on population ecology. Some fine examples of ecophysiological investigations are the contributions of the research group of Prof. RUDOLPH, Kiel (FRG), which focus on nitrogen metabolism in *Sphagnum* species. Also the papers on photosynthesis (see above) do well fit in the framework of this chapter although, unfortunately, in none of them any attention is paid to the aspect of bryophyte production.

Reproduction and dispersal ecology is the subject of the seventeen papers presented in chapter 2 (session convener H.J. DURING). The first contribution by MILES and LONGTON gives us a detailed insight in the life history of *Atrichum undulatum*, a nice product of a wide-ranging and ample study. Some other papers which may be mentioned here, are those by such noted experts as WHITEHOUSE (protonema-gemmae in European mosses), VAN ZANTEN and GRADSTEIN (long-distance transport) and MILLER (paleoecology).

The thirteen papers of session 3 (convener N.G. Slack) deal with community ecology. This chapter is rather illustrative for the historical development in the area of vegetation ecology. For instance, the here partly reprinted (and without any doubt important) work of ZÓLYOMI on cryptogamous synusia in Hungary, is an example of a study according to the classical method of the Braun-Blanquet School. On the other hand, most other papers are illustrative for the present day interests of vegetation ecologists, especially as to the use and comparison of different methods. Good examples are here the contributions of Orbán (use of bryophytes for ecological comparison), DURING and TER HORST (diversity and dynamics in bryophyte communities), GLIME, SLACK and MESTON (comparison between the Levins' and Freeman-Tukey niche width measures for bryophytes) and HOFFMANN (comparison between the relevé method and the plotless sample method for cryptogamous synusia).

Only five papers are presented in the chapter population ecology (session 4, convener R. WYATT). This number is remarkably low, even if we take into account the omission of ZIELINSKI's paper here (see above). As compared to higher plants, only few attention has been paid so far to the genetic variability in natural populations of bryophytes. This surely will change in the near future, enabled by a more frequent use of electrophoresis of proteins. The results in this field hitherto (in the present work for instance the papers of KRZAKOWA and BISCHLER, ODRZYKOSKI, WYATT, ODRZYKOSKI and STONEBURNER), indicate that there might be a much greater genetic variation in bryophyte populations than thought before (cf. SCHUSTER 1966: "The Hepaticae and Anthocerotae of North America", Vol. 1).

In the chapter after session 5 (convener R.E. LONGTON) eleven papers are presented on the subject bryophytes in ecosystems. A major part of them deals with bryophytes in sub-tropical and tropical ecosystems, especially the tropical rainforest. An understandable interest, particularly in the view of the continuous and rapid destruction of these natural environments. In their studies on neotropical Andean vegetations, both VAN REENEN and FRAHM pointed out that the total cover of bryophytes considerably increases from the tropical-lowland rainforest to the high-andean forest. FRAHM's experiments seem to confirm the hypothesis that this phenomenon is mainly determined by physiological factors, i.e. the combination of a high tempera-

ture and a low light intensity in the tropical-lowland rainforest, does not allow sufficient net photosynthesis. Two other appreciable papers here come from VASANDER (the effect of forest amelioration on the understorey biomass, species richness and diversity of southern-boreal Finnish mires) and SIMON (the leaf-area index of three moss species). Animal-bryophyte relations are discussed in the contributions of DAVIDSON and LONGTON (acceptability of mosses as food for a herbivore, the slug Arion hortensis) and GERSON (Mites which feed on mosses).

Bryophytes as bioindicators is the title of the last chapter. Conspicuously, all contributions on this subject are from European botanists. Not less than five papers come from the Ecology Department of Sarosiek (Wroclaw, Poland), who was the convener of this session. Without any exception, great attention is paid to the monitoring function of bryophytes in relation to environmental conditions. It must be said, that many of the papers published here, find their origin in the classical work of BARKMAN (1958): "Phytosociology and Ecology of Cryptogamic epiphytes." Two comprehensive contributions in this chapter are from MAKINEN, who used respectively Sphagnum spp. and Hylocomium splendens in air pollution monitoring studies in Finland.

Summarizing, it can be said that this book is a nice follow up of a successful conference; the first conference ever held, entirely devoted to bryoecology. Apart from some minor points (like the before mentioned incoherence of the chapter on physiological ecology; the relative high number of printing errors; scientific names which are underlined and not in italics), the book is rather handsome and has a fine layout. The four editors involved have made a good job in editing a book with more than 900 (!) pages, and for that they deserve our sincere compliments. I feel so, that this book will turn out to be a standard work for all those, not only bryologists, who are interested in the ecology of bryophytes. So I would like to recommend this book to all botanists who work on bryophytes or have a general interest in this group of plants.

J.L.D. MEENKS

GIVNISH, T.J. (ed.): On the economy of plant form and function. Cambridge University Press, Cambridge — London — New York 1986, 717 pp.

The "economy" involved in the title is a theme in vogue nowadays when the economic situation of the world gets worse. It is not by chance that the question of the "economicality" of organisms and life-functions is emphasized recently. The "economicality" is really an object of capital importance since an organism which has an "uneconomical" function cannot exist, and the life on the earth may use limited resources of material and energy as well.

The book contains the subject of the Sixth Maria Moors Cabot Symposium which was organized in Harvard Forest, U.S.A., during August 1983, under the title "Evolutionary Constraints on Primary Productivity: Adaptive Patterns of Energy Capture in Plants". 20 papers were presented under three principal topics. In the majority of the papers, the cost-benefit models play an important role. Many models assume that a plant's inclusive fitness will be maximized if its traits maximize the whole plant rate of energy capture, since a plant's rate of energy gain places important constraints on its competitive ability. Even a small difference can have a dramatic effect on a plant's competitive ability. In the papers the authors focus the impact of various plant traits on whole-plant growth and competitive ability.

In recent years several criticisms were arisen in opposition to cost-benefit models. In his introduction the editor enters into a controversy with these criticisms taking the principal counter arguments one after the other. We can get several useful information about the role of a plant's traits play in the adaptation of whole- plant by using of cost benefit models, although the difficulties are obvious.

Part I, Economics of gas exchange (13 chapters).

One of the articles deals with modifications of solar radiation absorption patterns and implications for carbon gain at the leaf level. "There are two specific leaf orientations that tend to enhance photosynthetic rate on a diurnal basis. The first is solar tracking, which may enhance productivity at the leaf level because of the resulting high incident irradiances, but limits total canopy productivity by restricting the maximum canopy leaf area index. The second is fixed leaves with steep leaf angles and oriental lamina in an east-west direction. This orientation tends to increase the incident irradiance and thus photosynthesis, early in the morning and again in the later afternoon. These are periods of the day when the transpirational demand is lowest" (EHLERINGER and WERK).

In the other articles themes which are directly connected with gas exchange are discussed: limitation of photosynthesis by nitrogen, form and orientation in relation to photosynthetically active radiation (PAR), interception by cacti and agaves, strategies of light absorption in rain forest herbs, optimal stomatal conductance, costs of a plant at the root system level, ecological patterns of xylem anatomy, adaptations for water and thermal balance in Andean giant rosette plants, etc.

In the tenth chapter, economy of symbiotic nitrogen fixation is discussed. "Symbiotic nitrogen fixation, though of obvious benefit to a species in situations in which soil nitrogen is limiting, incurs substantial penalties to a host plant in terms of cost of maintenance and functioning of symbiotic structures and their nitrogenase systems. Where nutrients other than N are also in short supply, a N_2 -fixing association will be advantageous only if it is able to acquire these limiting nutrients with the some effectiveness as do competing nonfixing plant species" (PATE).

Part II, Economics of support (6 chapters).

The themes are written up in this part: evolution of plant life forms, biomechanical constraints on crown geometry in forest herbs, the roles of carbon balance and branching pattern in the growth of woody species functional geometry of seaweeds, etc. One of the articles deals with branching patterns and angles in trees. There traits play important roles in establishing both crown form and leaf position. "Spatial models of branching patterns have been devised that account for complex tree form with relatively simple rules and few parameters of branching. In geometrically simple trees, like *Terminalia*, that have regular clustering of leaves at the tips of branch units, deterministic computer simulations have shown that the observed parameters of branching (asymmetrical angles, relative branch length, branch number per tier) are close to theoretical values that would optimize leaf packing" (Fisher).

Part III, Economics of biotic interactions (1 chapter).

In the only chapter of this part costs of plant's defense in opposition to herbivores are discussed. The cost of the carbon and energy for defensive compounds is proportional to photosynthetic rate and leaf allocation fraction. The nitrogen cost of defense compounds is highest in plants with low nitrogen contents. Thus, we would expect to see nitrogenous compounds produced only in plants with high overall nitrogen contents. However, such plants are most sensitive to the carbon costs of defense; so we would expect these nitrogenous compounds to be produced in small quantities in the plant, unless they have other functions" (GULNOR and MONEY).

The editor's surveys are got before the chapters of the parts. In these useful and valuable surveys GIVNISH describes the current state of research of the themes are given. A detailed bibliography follows each chapter. At the end of some chapters appendices help the readers to comprehend the mathematical demonstrations. Quick finding of the themes is helped by the index at the end of the book. The presentation is attractive with black and white photographs, line drawings and tables.

This book gives valuable information for plant breeders, biotechnologists, ecologists and physiologist. Students who are interested in this themes can use the book with many benefit, too.

Z. KOVÁCS

LIBBERT, E.: Lehrbuch der Pflanzenphysiologie. 4. Auflage. VEB Gustav Fischer Verlag, Jena 1987, 434 pp.

This is the fourth, enlarged edition of the widely-used textbook by Professor LIBBERT, of Wilhelm Pick University in Rostock.

The book covers the whole of plant physiology in wellbalanced depth and fullness. In accordance with the traditional arrangement, the sequence of subjects is: metabolism, the basic principles of biological regulation, special questions of metabolism, growth and development, movement.

Although the division is traditional, the contents are up-to-date. It can be stated indisputably that (even if its title did not indicate this) the book is meant for learning, and it fulfills this function.

The text is exact clear-cut, the author describes everything factually and quantitatively, and the figures are relevant, simple and well understandable. This is especially the case for the processes of the basic metabolism, and the questions connected with the metabolic and genetic regulation.

The author well exemplifies how he can summarize all the essentials of the basic principles, and the chemical of genetic processes.

The conciseness of the book, however, means at the same time that learning the material needs great energy and concentration. This is increased by the overdetailed structure, characterised best by the fact that almost every page contains the titles of several subchapters.

Although the textbook character has been emphasized, the work is much more than that. It can be a source of sure knowledge not only for students, but for practising plant physiologists too, especially in those cases when they have to consider facts lying outside their own research area.

The book is recommended to students, researchers and teachers of plant physiology, biochemistry, agrobiology and crop production.

F. ZSOLDOS

KLEINIG, H. — SITTE, P.: Zellbiologie. Ein Lehrbuch. Gustav Fischer Verlag, Stuttgart — New York 1984, 488 pp. 482 figures, 87 tables

Both authors work at the Institute of Cell Biology at Albert Ludwig University, Freiburg, FRG. The book covers all branches of contemporary cell biology. The main chapters are: 1. Cells and Organelles. Including: The Cell — Introduction, Biomembranes, The Plasmamembrane, The Cytoplasm, Ribosomes and Protein Synthesis, Intracellular Membranes. The Nucleus, Mitochondria and Respiration. Plastids and Photosynthesis, Cell Walls. 2. Specific Types

of Cell. Including: Muscle cells, Neurons, Rod cells and Photoreception, Blood and Blood Cells, Immun System, Tumor Cells. 3. Reproduction, Differentiation and the Evolution of Cells. 4. Appendix summarizing main techniques of cell biological studies.

Animal and plant cells are discussed throughout, botanical aspects and examples are presented whenever appropriate. Most interesting chapters for botanists are those discussing specific features of plant cells. Particular attention is paid to plasmodesmata, plastids and photosynthesis, cell wall, plant tumor cells, and some problems of cell differentiation in Acetabularia, Volvox and Dictyostelium. In addition to fundamental knowledge, new results and hypotheses on these problems are also presented. A great value of the book is its lucidly arranged material, of the highest quality. The volume, as a textbook, is written primarily for university and highschool students of cell biology, but is also recommended to biology teachers and experts of medical and agricultural sciences as well as all other wishing to be informed on the state of the art in cell biology.

L. FRIDVALSZKY

LEGENDRE, P., LEGENDRE, L. (eds): Developments in Numerical Ecology. Ecological Sciences Series Vol. 14., Springer, Berlin-Heidelberg, 1987, 585 pp.

During the last few decades the multivariate analyses became very popular among ecologists. These techniques proved to be very useful in several topics, including the discovery of community structure and niche relationships, ordination and classification of communities, etc. Generally they are the tools for simplifying complex, n -dimensional systems, and to help ecologists to generate hypotheses. In contrast with their widespread applications, detailed tests revealed some failures of these techniques, and therefore the need for better ones has been realised. There are three main directions of the development: (1) seeking for more robust analyses as enhanced linear, non-linear, and non-metric techniques, (2) seeking for the possibility to analyze more complex problems as multiway data sets, and (3) to construct appropriate numerical methods for exploring ecological information from special data e.g. binary or mixed variables, spatial points, and contour maps.

In the last few years, several new multivariate techniques have been introduced mainly by psychometricians, usefulness of these techniques have not been tested yet in ecology. The main goal of the workshop on numerical ecology held in Roscoff (France) in 1986 was to familiarize community ecologists with some of these new numerical tools and to promote the applicability of these methods to specific ecological problems. The meeting was organized by the editors of this book. The workshop had 51 participants from 14 countries. The book comprises the invited lectures and the working group reports. The invited lectures covered 5 different topics: (1) scaling techniques, (2) clustering under a priori models, (3) fractal theory, (4) path analysis for mixed variables, and (5) spatial analysis.

The term scaling techniques covers the ordination methods. In the first chapter J.C. GOWER presents a comprehensive review of these techniques, with special respect to the relevance of different types of data and measurement scales. J.D. CARROLL introduce the ecologists several types of metric and non-metric multidimensional scaling procedures. These analyses were developed at the AT T Bell Laboratories. Although these algorithms and programs have already been published in several books and papers, only a few of them have ever applied by the ecologists. These programs seem to

offer the most variable computational possibilities in multidimensional scaling available on the market (e.g. metric or non-metric technique, using similarities or dissimilarities, two- or three-way technique, individual weighting, external analysis). These procedures provide a lot of alternative strategies for the ecologist users, but one needs great experience to choose the best technique for a given study. The next paper of scalings by Y. ESCOUFIER focusses on the effects of scale, type of variables, weighting of statistical units in the case of principal component analysis. J. de Leeuw discusses the most important multivariate methods and he gives generalization of the casual linear techniques by allowing optimal non-linear transformations of variables. Non-linear multivariate analysis with optimal scaling supports a general framework to detect non-linear relationships. W.J. HEISER represents the unfolding technique, which allows dual projection of variables and objects in the ordination space. The clustering chapter contains three papers about some nonstandard algorithms like as fuzzy sets (by J.C. BEZDEK), constrained clustering (by P. LEGENDRE), and conditional clustering (by L.P. LEFKOVITCH). There is a good review on fractal theory by S. FRONTIER. Fractal analysis seems to be very useful to understand the geometry of nature in oceans and lakes, and to describe the animal movements. Fractal theory was created by the hydrobiologists, but as D. SIMBERLOFF et al. at the animal ecology working group of the workshop pointed out the assumptions of fractal theory rarely fit to the system studied. There is a chapter on path analysis with optimal scaling by J. DE LEEUW, and two others on spatial analysis. B. RIPLEY presents a brief general discussion on the methods for detecting an interaction between species. The paper by R.R. SOKAL and J.D. THOMSON discusses the methods of autocorrelation analysis and presents an example of two understory plants in the genus *Aralia*.

One of the most important parts of the book is the Working Group Reports. The methods described in the book are evaluated by different aspects. Working groups were organized in the following topics: microbial ecology, benthos studies, pelagic community studies, biological oceanography and limnology, terrestrial plant ecology, and terrestrial animal ecology.

It is surprising to see the scepticism of D. Simberloff and his co-workers at the animal ecology working group on the usefulness of ordination techniques in animal ecology. Almost there is no any other relevant technique to look into an n-dimensional community structure and to reveal complex animal-habitat relationships. It is true, plant ecologists seem to be more successful (or lucky) with the applications of ordinations, but (1) there were made much more attempts for their application than in animal ecology. I agree with the statement of D. SIMBERLOFF et al., that botanists were forced to use them, because a great part of their problems needed preliminary surveys of the structure. These methods are very helpful to the plant ecologists for hypothesis generation. (2) Traditionally botanists have been much more interested in multivariate techniques than zoologists. They often tried to apply new procedures, moreover they carefully tested the applicability of the techniques (see the huge pile of papers published both in *Vegetatio* and *Journal of Ecology*). The results of the efforts were the more correct applications than the earlier ones. A great part of their statements refers only to botanical problems. Similar methodological studies are badly needed in animal ecology, too.

In spite of the heterogeneity almost all parts of the book are easy-to-read. Some of the topic, others were tried to focus on special questions connected with a branch of methods. This book was a real excitement compare with the other ones appeared in multivariate analysis and quantitative ecology. Despite of the high price, this book is worth its value. I believe it offers a lot of good ideas both for methodological developing and for

applying numerical methods in ecology. I could highly recommend the book to community ecologists and especially to numerical ecologists.

CS. MOSKÁT

Algal Biomass Technologies. An Interdisciplinary Perspective. Eds: William R. Barclay and Robins P. McIntosh. Nova Hedwigia, Heft 83. J. Cramer, Berlin 1986.

This book is the proceedings of the "Workshop on the present status and future directions for biotechnologies based on algal biomass production" held at the University of Colorado, Boulder, on April 5-7, 1984.

The objective of the workshop and the proceedings is outlined by the editors in the introduction: "Since the energy crisis of 1973, the emerging biotechnology industry appears to be developing new approaches for the production of many of the petroleum based fuels and chemicals in current demand in the world today. Many of these new techniques are based on microbial processes utilizing new developments in genetic and biochemical engineering. While most of the current research has focused on bacterial and fungal systems, there is a clear need to extend this technology to algal systems. Algae represent a renewable, solar energy based resource that can be exploited for microbial biomass production."

The papers are classified into five groups, according to the main sections of the workshop:

Algal genetics and strain selection — 7 papers

Physiological and biochemical aspects of algal biomass production — 7 papers

Algae as a source of chemicals and natural products — 6 papers

Fuels from algal biomass — 5 papers

Technologies for mass algal culture separation and harvest — 10 papers

Each topic is followed by the discussion of papers during the workshop which also a brief up-to-date summary of results. The list of participants and their addresses and an index complete the volume.

It would be difficult to select separate topics or papers from the book; all of them present new results, in a more or less concise format, and showing future perspectives. It is well-known that many excellent results have been published in the field of biotechnology on algal genetics, cultivation of algae and their application as raw material, food or energy source; yet there are even more problems to solve. In a sense this is expressed by some introductory sentences of M. NEUSHUL, the leader of the session "Fuels from algal biomass": "There have been comments about the cultivation of algae being a cruel hoax, and all of us having fallacious dreams. I just hope that we live long enough for us to see these dreams proven. I think that people in this meeting are showing that these are not very fallacious dreams, and this is not a cruel hoax, maybe expensive."

This book is warmly recommended to algologists, theoretical and practical experts of biotechnology and to every researcher involved in studies on algal genetics, physiology and biochemistry. The proceedings will certainly contribute much to the development of new theoretical and practical results in this promising field of algology.

K.T. KISS

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Borhidi, A., Muñiz, O., Del Risco, E. 1979a: Clasificación fitocenológica de la vegetación de Cuba. Acta Bot. Hung. 25: 263–301.

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